CONSEIL PERMANENT INTERNATIONAL
POUR L'EXPLORATION DE LA MER
CHARLOTTENLUND SLOT – DANEMARK

JOURNAL DU CONSEIL

VOL. XXI · NO. 2

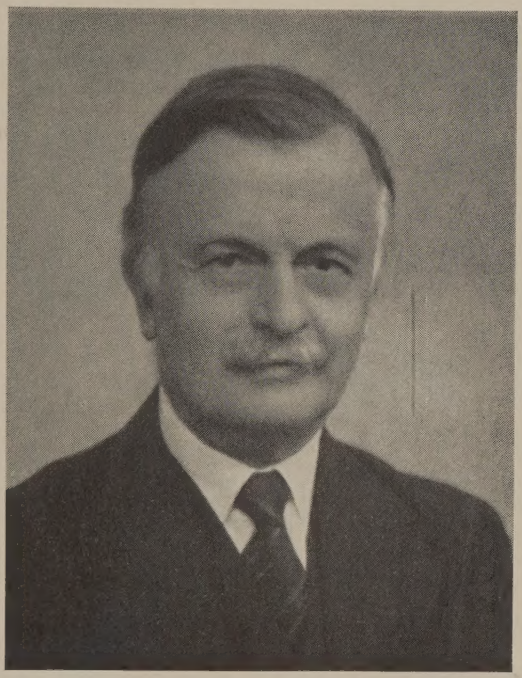
PUBLIÉ PAR LE BUREAU DU CONSEIL

RÉDIGÉ PAR
J. R. LUMBY

EN COMMISSION CHEZ
ANDR. FRED. HØST & FILS
COPENHAGUE

AVRIL 1956

IMPRIMERIE A/S L. IHRICH . COPENHAGUE



Haaken Hasberg Gran.

1870—1955.

H. H. GRAN passed away peacefully on 2nd June 1955, having retained his remarkable vitality until a few weeks before his death. When he celebrated his 85th birthday on 17th April with a reception at his home, it was evident that his health was declining and his numerous friends who were there felt that is was a time of farewell.

G r a n was born in Tønsberg in 1870, the son of a naval officer. Even as a boy he showed interest in natural science and he started his scientific studies while a student at the University of Oslo. As was fitting for a pupil of Professor

N. W i l l e, a prominent algologist, in his first publications he dealt with the benthic algae. His interest was soon diverted, however, towards the floating vegetation of the sea, and marine phytoplankton became the main field for his scientific studies throughout his life. It was a combination of fortunate circumstances which enabled G r a n to carry out important work in several fields of marine biology and so to secure himself a lasting position as one of the outstanding pioneers in marine plankton research.

A keen eye for morphological detail and a thorough training in systematics made him a first-class taxonomist, and his illustrations always bring out the "habitus" of the species, so difficult to reproduce. During his early years as a planktologist he described a large number of important phytoplankton species and in the diatom section of *Nordisches Plankton* he presented a diatom flora which served for a long time as the guide for students of northern waters.

Through his life-time collaboration with his close friend Johan H j o r t and with Fridtjof N a n s e n he had the opportunity to acquire first-hand knowledge of the sea and also to obtain material from the most varied regions. This happy period in Norwegian marine research further stimulated G r a n' s interest in the ecology of marine plants, which was already evident in his first studies, and it led to a clear conception of the interaction between organism and environment, which formed the background of all his studies of phytoplankton populations.

The thesis for his doctorate, "Das Plankton des Norwegischen Nordmeeres", presented in 1902, was based on material he had collected on the "Michael Sars" cruises organized by H j o r t. In this paper, G r a n stressed the ecological approach to an understanding of the regional and seasonal changes in the population. He replaced C l e v e' s explanation, that seasonal changes are due to the influx of water masses from distant regions, by a botanical conception, that changes in the composition of the phytoplankton are due mainly to local changes in the environment.

G r a n' s general view of the metabolism in the sea was based upon the ideas which G. O. S a r s had put forward as early as 1879 and which had been expressed later by B r a n d t, H e n s e n, L o h m a n n, and N a t h a n s o h n in more elaborate form. In 1905, after having been appointed to the Chair of Botany at the University of Oslo, G r a n taught plant physiology and for a short period he studied under Professor

W. Pfeffer, the prominent plant physiologist. This gave him a physiological background which brought him into fresh fields of research, but the backbone of his plankton work was always the survey, in which studies of the population were collated with hydrographical observations.

In his numerous publications we find studies on plankton populations from the most varied areas, from Japan and the west coast of North America, and from both arctic and antarctic regions; but his main field was the North Atlantic, with the Norwegian Sea and the coastal waters of Norway as the centre of his interest.

In his report on phytoplankton in Murray and Hjort's *The Depths of the Ocean* Gran not only discussed the results of the "Michael Sars" expedition in the North Atlantic, in which he participated, but also gave a general account of conditions of plant life in the open ocean. This work in particular demonstrates Gran's ability to combine knowledge of the most varied fields with a sound imagination, so important for progress in natural science.

Gran's reports on the international survey of the North Sea and the southern part of the Norwegian Sea, organized by the International Council for the Exploration of the Sea (1912), on his investigations of the spring phytoplankton development in the coastal waters off Lofoten and Møre (1929—31), and on the survey of the Bay of Fundy and Gulf of Maine (1935) are highly important contributions to our knowledge of conditions of plant production in northern waters.

Gran knew well that experimental studies are necessary to solve the problems raised by survey work. As early as 1907 he published his first attempts at determining the rate of reproduction in phytoplankton and, in subsequent studies, he tried to obtain information on the actual production of organic matter in the sea and on the excretion of organic matter by phytoplankton. His method for measuring production, worked out in collaboration with Professor T. Gaarder, is still in use, although it is being replaced by Steemann Nielsen's ^{14}C method.

While on a visit to Professor M. W. Bejerinck in Delft, Gran made the first study of bacteria which decompose agar-agar and also worked on nitrate-reducing bacteria in the sea.

He took part in the activities of the International Council from the first and was chairman of the Plankton Committee for many years. Having worked on zooplankton as well — he was the first to describe the various stages of *Calanus finmarchicus* — he was eminently qualified for this position.

Gran's stimulating personality and his positive attitude towards new ideas made it easy for him to make contact with the younger generation. Although he was a veteran in the Council, he was "young with the young ones" and maintained a tradition of non-specialization, preferring a thorough training in all the fields of oceanography with which problems of the fertility of the sea are concerned.

His clarity of mind and unconventional approach, which were Gran's characteristics in discussion, also made his publications so stimulating that his reputation became world-wide. Through his activities in the International Council and his visits to the United States and Canada he attracted pupils and collaborators from many countries. They will all treasure Gran's memory, not only as a prominent scientist, but also as a kind and charming friend. In human relationships, Gran was a worthy representative of *scientia amabilis*.

T. B.

The Determination and Occurrence of Nickel in Sea Water, Marine Organisms, and Sediments[1]).

By

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Introduction.

The objectives of this investigation were to (1) review the literature dealing with the occurrence of nickel in sea water and in marine organisms, and examine the methods previously used for the estimation of nickel in marine organisms, (2) devise a convenient and reliable method for the determination of minute quantities of nickel in natural waters, (3) determine the concentrations of nickel occurring in the waters of the Puget Sound region, and (4) investigate the occurrence of nickel in certain marine fish, plankton, and deposits of the Puget Sound region.

Previous Studies on the Occurrence of Nickel in Sea Water, Organisms, Sediments, and Rocks.

Relatively few analyses of nickel in sea water are given in the literature. The data available have been summarized in Table 1. The concentrations given range from 0·002 μg.-at. of nickel for the North Sea to 0·131 μg.-at. for Sevastopol Bay in the Black Sea. In most of the papers cited nothing is said about precautions taken to prevent contamination of the samples or corrections made for traces of nickel in the reagents utilized. The data available vary by more than one order of magnitude, and due to the meagreness of information it is impossible to state whether the differences are due to regional or seasonal variations, or to the sensitivities or errors in the methods employed for analysis.

[1]) Contribution No. 192 from Department of Oceanography, University of Washington, Seattle, Washington, U. S. A.

Table 1.

Amounts of nickel in water as reported by various investigators.

Place of collection	µg./Kg.	µg.-at./Kg.	Investigators and References
North Sea	0·12	·002	Ernst and Hörmann (1936)
Sea water (est.)	1·0	·017	Maljuga (1939)
Skagerak, Gullmarfjord	·5	·0085	I. and W. Noddack (1939)
Black Sea	6·0	·102	Maljuga (1942), according to Vinogradov (1944)
Sea water (est.)	3·0	·051	Vinogradov (1944)
Black Sea, 1700 m.	4·5	·076	Maljuga (1945)
Black Sea, Sevastopol Bay	7·7	·131	Maljuga (1945)
Black Sea, Karedag Biol. Stat.	5·1	·087	Maljuga (1945)
Barents Sea, off Yarnysh Bay	3·4	·058	Maljuga (1945)
Sea water, avg. (est.)	3·4	·058	Maljuga (1945)
20 miles off Plymouth, 20 m. depth, 22. II. 50	5·5	·093	Black and Mitchell (1952)
Ardencaple Bay, 0·5 m. depth, 25. VI. 50	1·5	·025	Black and Mitchell (1952)
Atlantic Bridge, 15 m. depth, 27. VI. 50	1·5	·025	Black and Mitchell (1952)
Pacific Ocean, off Shirahama, Wakayama, 20. X. 50.	0·75	·013	Ishibashi (1953)
Average:	3·4	·053	
River waters, average	4·8	·082	Maljuga (1945)
Lake waters, average	17	·29	Maljuga (1945)

The amount of nickel reported in materials of geologic or biologic origin by other investigators is given in Tables 2 and 3. These data show marked variation in the trace quantities of nickel in different rock formations. Besides meteorites and ore formations the basic igneous rocks, red clays and organic sediments are the richest in nickel, whereas acid igneous rocks, sedimentary rocks, soils and shallow water sediments have the lowest nickel content. Some oolitic iron ores are relatively high in nickel.

There are marked differences in the quantities of nickel in plants and animals. I. and W. Noddack (1939) state that the element must be essential for animal life because one kilogramme of dried organisms contained 41,000 times the amount of nickel contained in one kilogramme of sea water. They stated also that the concentration of cobalt in marine animals is about one-tenth that of the nickel concentration. Black and Mitchell (1952), employing similar reasoning, found a concentration factor of 540 for nickel in sea plants as compared to sea water. The concentration of cobalt was equivalent to about one-fourth that of the nickel concentration of the plants. They also noted that the nickel concentrations were higher in spore-forming *Laminaria* than in those not forming spores, and that greater quantities of nickel occur in the plants in the summer than in the winter months. On the other hand, Bertrand and Mâcheboeuf (1925) claimed that animals have far less nickel than cobalt in their tissues. Kent and

Table 2.

Amounts of nickel in rocks, soils, and sediments as reported by various investigators.

Element	Ni in mg./Kg.	Ni in mg.-at./Kg.	Investigators and References
Basic igneous rocks	65	1·1	Lundegårdh (1949)
	100—2,000	1·7—34·0	Vogt (1923)
Acid igneous rocks	tr.—5	tr.—·085	Vogt (1923)
	8	·14	Lundegårdh (1949)
Igneous rocks	80	1·4	Sandell, Goldich (1943)
	200	3·4	Clarke (1924)
	48	·82	Lundegårdh (1949)
	100	1·7	Goldsmidt (1937)
Oolitic iron ores	—39,000	—664	Maljuga (1939)
Sedimentary rocks	tr.—·28	tr.—·0048	Maljuga (1939)
Sandstones	2—8	·034—·14	Rankama, Sahama (1949)
Shales	24	·41	Rankama, Sahama (1949)
Limestones	0	0	Rankama, Sahama (1949)
Mineral soils	20	·34	Goldsmidt (1954)
Soils	8·3—730	·14—12·5	Maljuga (1939)
Meteorites	16,000	272	Rankama, Sahama (1949)
Asphalt	3,000	51	Wells (1946)
Naphtha	250—1	4·25—·017	DeGolyer (1924) quoted by Maljuga (1939)
Coal	220—5·2	3·7—·089	Kraut (1906)
Coal ash	700	12	Goldsmidt (1954)
Oak humus ash	100	1·7	Goldsmidt (1954)
Red clay (composite)	253	4·31	Clarke (1924)
Red clay (composite)	259	4·41	Young (1954)
Red clay, Pacific Ocean	164	2·79	Landergren (communication)
Terrigenous clays	498	8·49	Clarke (1924)
Sea deposits	250	4·25	Maljuga (1945)
Delta sediments	110	1·87	Maljuga (1945)
Near-shore sediments (composite)	47	0·8	Young (1954)
Manganese concretions	7,700	131	Irvine and Gibson, quoted by Maljuga (1945)

McCance (quoted by Monier-Williams, 1949) found that in humans much of the nickel consumed is discharged in the urine. Stiles (1946) states that nickel is more frequent in animals than cobalt, that nickel is irregularly distributed, and that little is known of its presence in various organs. He indicates that the availability of nickel to plants increases the growth but that there is no evidence that the element is essential. Wallace (1952) has demonstrated that excess nickel is toxic to plants and organisms and that its presence in excess may induce an iron deficiency. Vinogradov (1953) states that Paulais (1936) has found a concentration of nickel in the gills and liver of molluscs.

Goldsmidt (1954) assumed that divalent nickel accompanies divalent magnesium, cobalt, and iron because of the similarity of the ionic radii.

Table 3.

Amounts of nickel in plants and animals as reported by various investigators.

Element	Ni mg./Kg. Dry matter	Ni mg.-at./Kg. Dry matter	Investigators and References
Seaweeds	3·7	·063	Black and Mitchell (1952)
	·099—·83	·0017—·014	Maljuga (1939)
Marine plants	·5	·0085	Maljuga (1939)
Freshwater algae	·0017—·012	·00003—·0002	Maljuga (1939)
Fruits and grains	·01—2·0	·00017—·034	Maljuga (1939)
	·9	·015	Bertrand and Mokragnatz (19
Lettuce, cabbage, spinach, and peas	1·5—3·0	·026—·051	Bertrand and Mokragnatz (19
Pastures	·56—3·65	·01—·062	Scott and Mitchell (1943)
Whole plants on living basis	·013—1·5	·00022—·026	Maljuga (1939)
Calanus finmarchicus	1·2	·0204	Maljuga (1939)
Fish	·015	·00026	Bertrand and Mâcheboeuf (19
Osmerus eperlanus	·68	·0116	Bertrand and Mâcheboeuf (19
Gadus sp.	1·1	·0187	Maljuga (1945)
Polychaetes and molluscs	8—100	·14—1·7	Fox and Ramage (1931)
Mytilus edulis (meat)	2·35	·040	Bertrand and Mâcheboeuf (19
Sponges	1·8—6·14	·036—10·45	Bowen and Sutton (1951)
Marine animals	20·6	·35	I. and W. Noddack (1939)
	·5	·0085	Maljuga (1939)
	·01—20	·00017—·34	Maljuga (1939)
Land animals	·01—·05	·00017—·00085	Maljuga (1939)
Human liver	·09	·0015	Bertrand and Mâcheboeuf (19
Living matter	·01—20	·00017—·34	Vinogradov (1937)

The Determination of Nickel in Sea Water.

Ernst and Hörmann (1936) isolated nickel from the major constituents of sea water by adding a solution of a ferrous salt and then precipitating the ferrous and nickel sulphides with ammonium sulphide. Ishibashi *et al.* (1951) employed a ferric salt solution to serve as a collector, precipitating the traces of nickel with the ferric hydroxide by addition of ammonium hydroxide. Samples of 40 to 60 litres were taken for each analysis. Several other investigators used spectroscopic methods, concentrating samples of water by evaporation.

In the present investigation, the addition of a collector was unnecessary, because in an alkaline solution the traces of nickel were carried down with the precipitates of magnesium hydroxide or carbonate. The first reagent employed was sodium hydroxide, but this proved unsatisfactory because the analytical grade chemical contained as much as one microgramme of nickel per gramme. Sodium carbonate was obtainable practically free of nickel, and this was the reagent used. For the final estimation of nickel the procedure given by Sandell (1950) was employed. The complete procedure is as follows:—

Collection of samples.

Extreme care was exercised in the collection of samples to prevent contamination. The water-sampling bottle described by Thompson and Chow (1955) insured the collection of samples at various depths free of contamination. Samples were treated for analysis immediately after collection. If this were not done, micro-organisms in the water would continue to grow and take up nickel from solution.

Chemicals.

All chemicals should be completely free of traces of nickel or blank determinations made to ascertain the quantities of nickel present.

Sodium carbonate solution:	50 g. of reagent grade anhydrous sodium carbonate dissolved in 1 litre of distilled water.
Hydrochloric acid:	Solutions of 6N and 0·6N prepared by dilution.
Ammonium hydroxide:	Concentrated reagent grade.
Dimethylglyoxime:	A 1 % solution is prepared by dissolving in ethyl alcohol.
Bromine water:	Saturated solution.
Sodium citrate solution:	A 10 % solution prepared by dissolving the salt in water.
Chloroform:	Reagent grade.

Preparation of standard nickel solutions.

Weigh out exactly 0·3365 g. of nickel ammonium sulphate hexahydrate crystals or 0·0500 g. of pure nickel wire. Dissolve the salt in redistilled water or the wire in dilute nitric acid, transfer quantitatively to a volumetric flask, and dilute to one litre. Ten ml. of this solution is taken and diluted to exactly one litre. One ml. of the latter solution is equivalent to 0·5 microgrammes of nickel (0·0085 μg.-at./ml.).

Pure nickel wire is the most desirable substance to employ for preparation of standard solutions. Other standard solutions were prepared with the hexahydrates of nickel chloride, nickel sulphate, and nickel ammonium sulphate. The results obtained from the different standards are illustrated in Figure 1 and show that of the hydrates, if it is necessary to use one as a standard, nickel ammonium sulphate is preferable.

Procedure.

Two-litre samples of sea water are filtered through a type HA millipore filter. The filtrate is assumed to contain all the nickel in true solution (Lewis and Goldberg, 1954), whereas the detritus retained on the filter may be taken and analysed for nickel, as described later, and reported as particulate nickel.

One hundred ml. of sodium carbonate solution is added to the

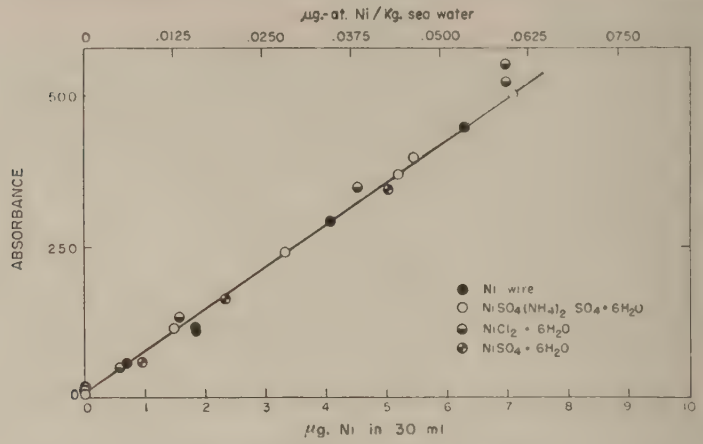

Figure 1. Nickel calibration graph.

filtrate which is then allowed to stand for about 12 hours. The supernatant liquor is syphoned through a millipore filter, and then the bulk of the precipitate is transferred to the filter. The residual precipitate is dissolved in a small quantity of 6N hydrochloric acid, the solution transferred to a small beaker to which the bulk of the precipitate retained by the filter has been introduced. The filter is then washed quantitatively with 6N hydrochloric acid and the washings combined with the solution resulting from dissolving of the precipitate. The total volume should not exceed 25 ml. and should be kept constant. This solution, after the addition of 15 ml. sodium citrate solution is made ammoniacal to a pH 8. It is then cooled rapidly, transferred to a separatory funnel, 2 ml. dimethylglyoxime added, and then shaken with 3 ml. chloroform for about half a minute. The chloroform extracts the nickel dimethylglyoxime. It is drawn off into another separatory funnel, care being taken not to permit any of a possible slight precipitate that may have formed over the chloroform to pass into the funnel. This process of extraction is repeated twice. The combined extractions are then shaken with 5 ml. 1 : 50 ammonium hydroxide and the chloroform drained into another separatory funnel. The ammonium hydroxide is shaken with 2 ml. chloroform and the latter drained and combined with the previous chloroform solution. This solution is then shaken with 5 ml. 0·6N hydrochloric acid, the nickel dissolving in the acid and the dimethylglyoxime being retained by the chloroform. The process is repeated. The combined solutions are then transferred to a flask which will permit eventual dilution to a volume of exactly 30 ml. Ten drops of bromine water are added, and after a few minutes ammonium hydroxide is slowly introduced until the bromine colour disappears. When this occurs, 0·5 ml. ammonium hydroxide is added in excess, followed by the addition of one ml. dimethylglyoxime and the

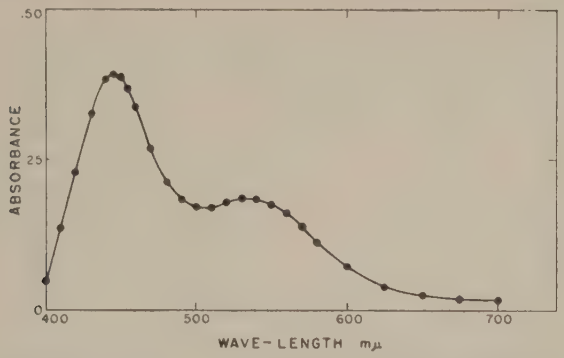

Figure 2. Absorbance of nickelic dimethylglyoxime complex.

solution made up to a volume of exactly 30 ml. It is then transferred to a 100 mm. cell and its absorbancy determined with a Beckman spectrophotometer. The absorbancy of the solution is measured at 450 mμ. The full colour intensity develops almost immediately upon the addition of dimethylglyoxime. The measurement of the absorbancy is made 15 minutes after the addition of this reagent and transference to the cell.

Preparation of calibration graph.

Varying quantities of the standard nickel solution are pipetted into separatory funnels so that a range of from 0·5 to 10 microgrammes (0·0085—0·170 microgramme atoms) of nickel are in six solutions. A volume of hydrochloric acid, equivalent to that used in dissolving the precipitated carbonates as described above, is added to each solution. Fifteen ml. of sodium citrate is introduced and each of the standard samples is treated in the same manner as given in the procedure, using the identical reagents in the same quantities. The absorbancies obtained are plotted against the concentration of nickel. From this graph (Figure 1) and from the absorbancies obtained on the water samples being analysed, the actual concentration of nickel may be ascertained. Figure 2 shows the absorbancy plotted against the wave-length.

By treatment of the standards in the manner described, there was compensation for errors occurring during the extraction processes and also for traces of impurities that might have been present in the reagents used.

Comparison and validity of procedures.

The method of Ishibashi *et al.* (1951) was questioned, as complete retention of nickel by the ferric hydroxide precipitate might not occur because of the exceedingly small concentration of nickel in sea water and the tendency to form soluble nickel ammonia ions. A comparison of the Ishibashi procedure with the method proposed was made, using, however, only two litres of water instead of 60 litres

required by Ishibashi. A sample of sea water was analysed with ferric hydroxide used as the collector in an ammoniacal solution. Nickel was also determined on a similar two-litre sample by precipitating the collectors already present in the water with sodium carbonate. In each case check determinations were made and the following results were obtained:—

	Microgramme-atoms nickel per Kg. of sea water		
	Portion A	Portion B	Average
Method of Ishibashi *et al.*	·015	·017	·016
Sodium carbonate method	·0255	·024	·025

These results demonstrate that greater quantities of nickel were precipitated when the natural collectors and sodium carbonate were used than when ferric hydroxide in ammoniacal solution was employed.

When a solution containing nickel is made ammoniacal, the very soluble nickel ammonia ion tends to form. However, in the presence of ferrous or ferric hydroxides most of the nickel will be retained by the precipitates, but due to the exceedingly small concentration of nickel occurring in sea water the precipitation is not quantitative.

To test further the validity of the sodium carbonate procedure, it was first deemed desirable to prepare a synthetic sea water, free of nickel, and to which known concentrations of nickel could be added. However, the synthetic sea water prepared contained nickel (present as an impurity in the chemicals used) in quantities far greater than the natural sea water and the concentrations of nickel proposed for addition, even though reagent grade chemicals were employed. Therefore, several different samples of natural sea water were analysed for nickel, varying concentrations of known amounts of nickel were then added to other samples of the same waters, and the total nickel was determined. The results were as follows:—

Ni in 2 litres sea water μg.-at.	Ni added μg.-at.	Ni recovered μg.-at.	Percentage recovered
·055	·085	·123	80
·055	·1365	·169	83
·055	·085	·143	103
·055	·085	·136	95
·0485	·085	·146	115
·053	·0425	·095	99
		Mean recovery:	96

Influence of storage on the nickel content of water.

It is well known that storage of samples of sea water before analysis markedly affects the concentration of some of the nutrient salts. It was found that the concentration of nickel was affected similarly.

Large samples of water were collected and divided in five portions. One portion was filtered and analysed immediately for nickel. Other portions were stored in darkness or subjected to the action of artificial illumination for a period of two to three weeks before filtration and

analysis. To another portion hydrochloric acid was added before storage and to still another carbon disulphide. The final analyses of these various portions yielded the following results:—

	Sample I	Sample II
	μg.-at. Ni/Kg.	
Immediate filtration and analysis	0·036	0·031
Storage in darkness for 3 weeks	·010	
Storage in darkness for 2 weeks		·028
Storage in light for 3 weeks	·026	
Storage in light for 2 weeks		·024
Addition of 7·5 ml. 12N HCl per litre before storage. Stored for 3 weeks	·041	
Stored for 2 weeks		·045
Addition of several drops of CS_2 before storage. Stored for 3 weeks	·016	
Stored for 2 weeks		·022

These results demonstrate that nickel is removed from solution by biological action on storage. The addition of hydrochloric acid halted biological action but caused some of the particulate nickel to go into solution, whereas carbon disulphide may have caused precipitation of some of the nickel. Thus filtration and analysis immediately after collection of samples is essential if one wishes to differentiate between the nickel actually in solution and particulate nickel. If one is interested solely in the total nickel content of a sample, then immediately after collection, two litres of the sample should be measured, transferred to an appropriate container, and 100 ml. of sodium carbonate solution added. Continuation of the analysis may then proceed according to convenience.

Determination of Nickel in Marine Organisms.

Two methods for the preliminary treatment of various samples of biological origin prior to the determination of nickel were studied, namely, direct ashing and wet combustion. The results, with the two methods used for destruction of organic matter, as evidenced by the amount of nickel actually determined, are given in Table 4. In all materials, with the exception of plankton, abnormally low results were secured on samples that had been ashed. Due to the high mineral content of plankton (as indicated by the voluminous and porous residue obtained on ignition) there were only slight differences observed in the results obtained by the two methods.

When wet combustion was deemed advantageous, the following procedure was used:— 2 to 8 g. of oven-dried material were weighed in an Erlenmeyer flask, treated with nickel-free concentrated sulphuric acid, and heat applied until the mass was colourless or yellow-brown. When all organic matter had been destroyed and much of the excess sulphuric acid fumed off, the residue was cooled and then treated with 10 ml. 6N hydrochloric acid. The solution was diluted to about 25 ml., heated again, and any residue was removed by filtration, the filtrate

Table 4.

Comparison between ashing and wet combustion of biological materials.

	Ni in mg.-at./Kg. dry matter	
	Wet combustion	Ashing
Plankton	·104	·101
Mackerel meat	·005	·0035
Perch meat	·007	·0035
Kelp	·012	·007
Dorsal skin from flounder	·017	·0085

being received in a separatory funnel. Fifteen ml. of sodium citrate solution was then added, and the analysis for nickel was continued as described above. The sulphuric acid used for wet combustion should be analysed for nickel by performing several blank determinations, and the correction applied.

Analytical Results.

Nickel in solution in sea water.

In Table 5 are given the results obtained on samples of filtered and unfiltered sea water collected in Puget Sound and adjacent areas. The mean value found for filtered sea water was ·034 microgramme atoms of nickel per kilogramme of sea water; extreme values varied from 0·024 microgramme atoms for a water collected at the surface in Hood Canal in May 1954 to 0·046 microgramme atoms for a sample secured from 35 metres in Puget Sound off Golden Gardens in October 1954. These data are more than one order of magnitude higher than the values given by Ernst and Hörmann (1936) and twice as great as those cited by Ishibashi (1953) but are in agreement with the concentrations given by Black and Mitchell (1952).

From the data given in Table 5, it appears that the concentration of nickel in the surface waters is less than that obtained in waters of the depths. A seasonal variation in the concentration of nickel, and that nickel is not a limiting factor in organic production, are also indicated.

Interstitial water.

Water was collected from holes dug in several mud flats during low tide. The nickel content, as indicated from data presented in Table 5, was slightly higher than that of the adjacent waters.

River and lake water.

Samples of water taken from Lake Washington and two rivers, the Hoh and Sol Duc, were analysed for nickel, and the data given in Table 5 show that the nickel content of these fresh waters was slightly lower than that of sea water.

Table 5.

Nickel content of waters in Puget Sound and adjacent areas.

Date of collection	Place of collection	Depth m.	Cl ‰	Soluble Ni μg.-at./Kg.
1954				
16. April	San Juan Archipelago, off McConnell Island	0	16·3	0·027
22. May	Hood Canal, off Misery Point	0	14·0	·024
		100	16·3	·027
7. July	San Juan Archipelago, Friday Harbor	0	16·2	·029
12. October	Puget Sound, off Golden Gardens, Seattle	0	14·9	·036
		35	16·6	·046
		80	16·6	·037
21. October		35—40	16·5	·044
3. November	Puget Sound, off West Point	0	16·4	·027
		75	16·7	·032
1955		150	16·8	·046
7. January	Puget Sound, off Point No Point	0	15·9	·030
				Total Ni μg.-at./Kg.
5. January	47°16′N., 127°04′W	0	17·82	0·048
		50	17·83	·041
		100	18·55	·054
		200	18·66	·034
6. January	Strait of Juan de Fuca, off Race Rocks	0	17·30	·034
				Soluble Ni μg.-at./Kg.
1954	Fresh Waters			
21. October	Lake Washington	0	0	0·026
20. December	Hoh River, Olympic Peninsula		0	·027
	Sol Duc River, Olympic Peninsula		0	·029
	Interstitial Waters from Mud Flats			
22. May	Head of Hood Canal			
	Water from surface of mud		9·0	0·031
	Hole dug at low tide mark		6·0	·039
	Brown Island, Friday Harbor			
	Hole dug in mud at high tide mark		16·3	·039
	Hole dug in mud at low tide mark		16·2	·024

Particulate nickel.

The residues retained by the millipore filters were analysed for nickel and the quantities reported as particulate nickel per kilogramme of water. The results obtained on detritus are shown in Table 6. The amount of particulate nickel averaged about 0·005 microgramme atoms per kilogramme of water, or about 15 % of the concentration of the soluble nickel.

Table 6.

Particulate nickel in water from Puget Sound and adjoining areas.

Date of collection	Place of collection	Depth m.	Ni μg.-at./Kg of sea water
1954			
16. April	San Juan Archipelago, off McConnell Island	0	0·007
12. October	Puget Sound, off Golden Gardens, Seattle	0	·003
		35	·007
		80	·003
21. October		35—40	·003
3. November	Puget Sound, off West Point	0	·005
		75	·007
		150	·007
21. October	Fresh water from Lake Washington	0	·005
20. December	Hoh River, Olympic Peninsula		·154
	Sol Duc River, Olympic Peninsula		·021

The particulate nickel in the waters of the two rivers investigated was considerably higher than that found in sea water, as shown by the data in Table 5. The Hoh River water contained much finely divided clay in suspension and the particulate nickel was much higher than that of the Sol Duc. The nickel present was of mineral origin.

The relatively high concentration of nickel in the particulate matter, as compared with the soluble nickel, gives an explanation of the very high values reported by M a l j u g a (1939, 1945) for river and lake water, as this investigator did not distinguish between soluble and particulate nickel.

Nickel in marine plankton.

The concentration of nickel in marine plankton is given in Table 7. The plankton was collected with metal-free nets, the major components determined under a binocular microscope, and the abundance reported as percentage by volume. The plankton samples were ashed before analyses for nickel were made.

F l e m i n g (1940) reported that in general one gramme of dry plankton is equivalent to 16 g. of fresh plankton. In accumulating the data given in Table 7, this statement was substantiated; but, as would be expected, there is a deviation from each particular sample depending upon its biological composition.

From the data presented, it appears that plankton collected in the spring months contains more nickel than that secured in the autumn. The nickel content of plankton collected at or near the surface showed a concentration of nickel twice that of samples obtained in deeper water. The concentration factor of nickel in fresh plankton in relation to the concentration of nickel in sea water was found to vary from 170 : 1 to 970 : 1 with an average value about 500 : 1. The corresponding concentration factor for phosphates is about 20,000 : 1. This shows that plankton organisms are highly selective as to intake of ions.

Table 7.

Nickel content of marine plankton.

Date of collection	Place of collection	Depth m.	% dry matter	Constituents by volume %		Ni mg.-at./Kg. dry matter
1954						
24. April	Puget Sound, off Golden Gardens, Seattle	0	8·4	*Pseudocalanus*	85	·525
				Acartia	10	
		50—75	8·1	*Pseudocalanus*	70	·262
				Sagitta	25	
23. May	Hood Canal, off Misery Point	0	12·5	*Peridinium*	60	·213
				Coscinodiscus	28	
				Pseudocalanus	8	
		70	9·6	*Coscinodiscus*	60	·136
				Pseudocalanus	30	
2. July	San Juan Archipelago, East Sound			*Schröderiella* and *Chaetoceras*	85	·174
		0	4·8	Other diatoms	13	
		10	6·0	*Schröderiella* and other diatoms	70	·094
				Ceratium	30	
15. October	Puget Sound, off Golden Gardens, Seattle	1	—	*Coscinodiscus*	90	·153
		40	—	*Coscinodiscus*	90	·101

In the Annual Report of the Institute for Seaweed Research (1953) it is stated that cobalt is assimilated by seaweeds during the processes of photosynthesis and emitted during the hours of darkness. As nickel is analogous to cobalt a preliminary test was performed in order to ascertain whether a similar behaviour could be noted, and thus give a possible explanation of the higher nickel content of surface plankton. Samples of sea water were taken, enriched by the addition of nickel, and living plankton was added. One bottle was placed in darkness for 30 hours and the other exposed to artificial light for a similar length of time. On filtration and the analysis of the waters, the following results were obtained:—

	Sea water Ni μg.-at./Kg.	Plankton and bacteria Ni μg.-at./g. dried material
Original nickel-enriched water	0·073	0·078
After 30 hours exposure to light with plankton	·025	·204
After 30 hours in darkness with plankton	·027	·150

These results demonstrate that besides the intake of nickel by photosynthetic activities, the decrease in concentration of nickel in the water may be attributed to selective adsorption or absorption or to assimilation by bacteria. It was noted that there was a decided growth of bacteria in the bottles after standing 30 hours. Bowen and Sutton (1951)

Table 8.
Nickel in fish.

	Length in cm.	Age years	% Dry matter	Ni in μg.-at./ dry matter
Fish				
Phanerodon tureatus (flesh)	32·5	7+	15·4	7·0
Phanerodon tureatus (flesh)	23·0	3+	21·7	6·0
Taeniotoca lateralis (flesh)	20·0	2+	19·6	7·0
Pneumatophorus diego (flesh)	24·0		28·6	5·5
Pneumatophorus diego (flesh)	33·0		28·6	5·5
Platichtys stellatus (flesh)	29·5	5+		9·2
Platichtys stellatus (dorsal skin)				17·0
Oncorhynchus kisutch (flesh)	58·0	2+		28·9
Oncorhynchus kisutch (sperm)				20·3
Oncorhynchus kisutch (blood)				13·5
Oncorhynchus kisutch (liver)				8·5
Sardinops caerulea				5·1
Molluscs				
Siliqua patula (flesh)				12·6

Most of the above specimens were collected and identified by Dr. Lauren R. Donaldson and Dr. Allan C. DeLacy, of the School of Fisheries, University of Washington, and John S. Thompson, of the Washington State Department of Fisheries.

assumed that bacteria associated with marine sponges could concentrate nickel in much greater quantities than the sponges free of bacteria. Ericson and Lewis (1953) made a similar assumption for the assimilation of cobalt by bacteria attached to seaweeds.

Nickel in marine plants.

Some plants were collected in the late spring and early summer of 1954 and prepared for analysis by ashing of the material. No detailed data are here presented because of the unreliability of the analyses due to ashing. The mean concentration of nickel in the plants examined by this method was 85 microgramme atoms per kilogramme of dried material; but as shown in Table 4, this average figure is low because of ashing.

Nickel in fish.

Analyses for nickel on several species of fish were made, and the data are given in Table 8. The flesh of *Oncorhynchus kisutch* contained about three times the concentration of nickel as found in that of the other fish examined, and about twice that of the molluscs analysed. The nickel content found in the flesh of the fish examined, with the exception of *Oncorhynchus kisutch*, is the same order of magnitude as that reported by Maljuga (1939) for marine animals.

Nickel in calcareous skeletons of plants and animals.

As Rankama and Sahama (1949) report the absence of nickel in limestone, it was deemed desirable to ascertain the absence of the

Table 9.

Nickel in calcareous skeletons of plants and animals.

	Place of collection	Ni μg.-at./Kg.
Plants		
Coralliniaceae (*Lithothamnion* and other genera)	Off Sarasota, Florida	70
Animals		
Macoma nubilus	Puget Sound	5·3
Pecten diegensis	Puget Sound	7·8
Mytilus californiensis	Puget Sound	6·0

metal in biogen calcareous remains. A few analyses were made on recent clam shells and calcareous algae. The results are reported in Table 9 and show the same tenfold difference as given above for the nickel content of plants and animals. From this limited data, it might be concluded that plants and animals concentrate nickel in the calcareous skeletons in the same degree as in their organic tissues.

Nickel in marine sedimentary deposits.

Samples of marine sediments from different areas were examined for their nickel content, and the results secured are shown in Table 10.

Two of the samples analysed were shallow-water sediments from the coast of Florida and were supplied by Dr. Howard G o u l d. The composition as well as the nickel content of these samples are comparable to sandstone. The sample from Charlotte Harbor contained more nickel than that from Tampa Bay and was also richer in organic matter, which may possibly explain the higher nickel content.

The sediment samples from Puget Sound and the adjacent Strait of Juan de Fuca and San Juan Archipelago are comparable, because of their composition, to the shales (Table 2) but have a higher nickel content. This high nickel content may be attributed to organic matter and to the adsorption of nickel ions by clay particles. The source of nickel, aside from that occurring in the inflowing waters, may be the result of freshwater runoff and the weathering and halmirolysis of rocks. This influx of nickel is removed from the surface layers by organisms or by adsorption by clay particles. A portion of these nickel scavengers eventually become sedimentized.

A series of sediment samples was collected on a course from near the entrance of the Strait of Juan de Fuca, across the continental shelf to the deep water of the Pacific. These results, given in Table 10, demonstrate that the nickel content of the sediments appreciably increases seaward. It may be assumed that nickel is halmirolysed from shallow-water sediments (Y o u n g, 1954) and enriched in deep-sea deposits by scavenging manganic hydroxide (G o l d b e r g, 1954). As indicated above, organic matter, clay minerals, and iron hydroxide may be as effective scavengers as manganese hydroxide. Further evidence of the effectiveness of iron as a scavenger is indicated by the high nickel content of marine oolitic iron ores. From the data given in Table 9 it

Table 10.

Nickel content of marine sediments.

Place of collection	Depth m.	Description of sediment	Ni mg.-at./Kg
Florida			
Tampa Bay	3	Quartz sand	0·024
Charlotte Harbor	3·5	Sandy mud	·082
Puget Sound Area			
Carr Inlet, Still Harbor	112	Silty clay and mud	·62
Hood Canal	148	Silty clay and mud	·66
Jefferson Head	278	Silty clay and mud	·75
San Juan Archipelago			
East Sound, Orcas Island	25	Silty organic mud	·57
San Juan Canal	75	Silty clay and mud	·62
Strait of Juan de Fuca			
48°13′N., 122°53′W.	46	Gravel and organic matter	·95
48°14′N., 123°24′W.	127	Sandy mud	·51
48°17′N., 124°02′W.	188	Sand	·36
North-east Pacific Ocean, Continental Shelf			
47°45′N., 125°02′W.	141	Sand and silt	·54
47°46′N., 125°05′W.	208	Sandy silt	·53
48°06′N., 125°10′W.	456	Silt and clay	·63
47°55′N., 125°30′W.	640	Clay	·87
47°50′N., 125°35′W.	841	Clay	·94
47°50′N., 125°43′W.	1180	Clay	·81
47°50′N., 125°48′W.	1490	Clay	1·05
47°54′N., 126°06′W.	1848	Clay	1·10
Gulf of Alaska			
53°15′N., 149°20′W.	4390	Diatom ooze 2—4 cm. below sediment surface	1·82
54°08′N., 141°15′W.	3620	Diatom ooze with red clay 2—4 cm. from sediment surface	2·90
54°08′N., 141°15′W.	3620	Foram ooze 110—112 cm. from sediment surface	·66
56°14′N., 152°58′W.	970	Terrigenous clay 55—57 cm. below sediment surface	·68
Bering and Chuckchee Seas			
74°14′N., 162°47′W.	30		·13
70°55′N., 158°67′W.	25		·17
68°19′N., 166°41′W.	20		·45
66°12′N., 162°40′W.	14		·51

appears that the formation of calcareous material also may be considered as a scavenger of nickel. Such being the case, the nickel in the calcareous debris will be subjected to halmirolysis.

In such a complex system as exists on or near the sea floor, halmirolysed nickel will tend to be reprecipitated or re-adsorbed by substances giving a more stable and less soluble form. Thus calcium

carbonate is subjected to a slow re-arrangement because of the chemical nature of the carbonate-bicarbonate-carbonic acid system. Some of the nickel liberated will be scavenged by the iron or manganese compounds, becoming very insoluble because of the characteristics of the iron or manganese compounds and the basic nature of the system.

Acknowledgement.

The authors wish to express their appreciation for financial assistance from the Office of Naval Research[1]), to Mr. Lew Dodd, of Yellow Island in the San Juan Islands, for collecting water samples, and to their colleagues in the Department of Oceanography for many suggestions and criticisms.

Summary.

Methods for the analysis of nickel in sea water, in particulate material, and in marine organisms were investigated and modified. By using collectors already present in sea water and sodium carbonate solution as the precipitant, a more satisfactory recovery of nickel was obtained. In the preliminary treatment of marine organisms for nickel analysis, wet combustion was preferred to direct ashing as a relatively large proportion of nickel appears to be carried off with the smoke. As nickel may be removed from solution by biological activity, samples of water should be treated immediately after sampling. Sea water from Puget Sound and adjacent areas contain about 0·034 μg.-at. of nickel per kilogramme in solution and 0·005 μg.-at. of nickel as particulate. River and lake waters contain slightly less soluble nickel than is found in sea water. The plankton examined contained twice as much nickel as the higher marine plants and more than ten times the amount found in the fish and molluscs examined. Indications are that plankton collected in the euphotic layers contained about twice the concentration found near the aphotic zone, and that nickel is probably concentrated by bacteria. Plants and animals concentrate nickel in their calcareous skeletons in the same degree as in soft organic tissues.

The amount of nickel in the sediments collected across the continental shelf to the deep sea increased as the depth of water and distance from shore increased.

Nickel is halmirolysed from shallow-water sediments and enriched in deep-sea deposits by several scavengers.

[1]) Contract No. N80NR-520/III, Project NR083-012.

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Time and Duration of the Spawning Season in some Marine Teleosts in Relation to their Distribution.

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As part of a study of the biology of the common shore fishes *Blennius pholis* and *Centronotus gunnellus*, the times and durations of the breeding seasons were determined and the cycles of maturation and depletion of the gonads were followed throughout the year. It then appeared that the breeding cycles of the two species are very different. *B. pholis* breeds for about five months, in late spring and early summer. A nest of this species (a crevice, or space between stones, guarded by the male parent) was usually found to contain more than one batch of eggs. The stage of development varied between the different batches, showing that they had been deposited at different times. Gonad examination of monthly samples collected in the field showed that the ovaries did not become spent after early spawnings, and observations in aquaria confirmed that each individual spawns several times during the breeding season. *C. gunnellus*, however, breeds for only about two months, in late winter or early spring. In this species each egg mass consisted of eggs all at the same stage of development. The egg masses of this species are guarded mainly by the females, though both parents are found guarding them early in the spawning season. Guardian females were always found to be completely spent, and could not therefore have spawned again for a year. In this species it was clear that the entire annual egg-production of each female was being concentrated into a single spawning act.

To investigate whether the size distribution of oocytes, in maturing ovaries of the two species, would show corresponding peculiarities, ovaries of *C. gunnellus*, collected in November, and of *B. pholis* collected in March, were fixed in Bouin's fluid. After dehydration and clearing,

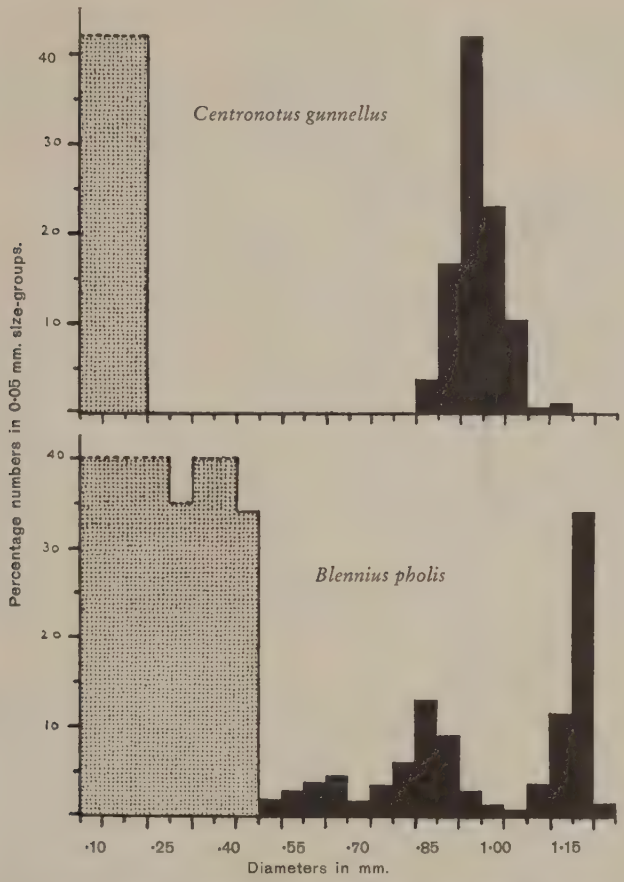

Figure 1. Size-distribution of maturing oocytes (black histograms) in ovaries of *Centronotus gunnellus* and *Blennius pholis*. The shaded areas indicate the sizes of small, apparently yolkless cells, which probably included follicle cells and oogonia. These were much more numerous than the oocytes, and they were therefore disregarded when calculating percentage size-distribution of the latter.

the ovaries were carefully opened in watch glasses and the oocytes removed and measured under a micrometer eye-piece. The percentages falling in each ·05 mm. size-range are given in Figure 1. It is evident from the curves than in *C. gunnellus* there is a single stock of large oocytes which might all be spawned together. In *B. pholis*, on the other hand, the oocytes are of a wide range, evidently destined to be matured and shed periodically during the season.

Table 1.

Northern species (arctic-boreal)	Limits of Atlantic distribution	Known breeding range (European)
Centronotus gunnellus (Gunnel)	Spitsbergen to English Channel. Greenland, Labrador to Woods Hole and Massachusetts (Sæmundsson, 1949; Duncker & Mohr, 1928; Breder, 1948).	Iceland (Sæmundsson, 1949); North Sea (Ehrenbaum, 1904); British coasts (Smith, 1887), and probably in English Channel.
Clupea harengus (Herring)	Spitsbergen to Bay of Biscay. Greenland to Cape Hatteras and rarely around New York (Sæmundsson, 1949; Hodgson, 1934; Breder, 1948).	Barents Sea (Rass, 1936); northern Norway (Hjort, 1914); Iceland to English Channel (Sæmundsson, 1949; Hodgson, 1934).
Cottus scorpius (Sea scorpion)	Spitsbergen to English Channel. Greenland and various North American coasts (Sæmundsson, 1949; Ehrenbaum, 1932).	Iceland (Sæmundsson, 1949); North Sea (Ehrenbaum, 1904); British coasts (Jenkins, 1936), and probably in English Channel.
Gadus aeglefinus (Haddock)	Spitsbergen to Bay of Biscay. Greenland to Cape Hatteras and New Jersey (Sæmundsson, 1949; Hjort, 1912; Breder, 1948).	Barents Sea (Rass, 1936); northern Norway (Raitt, 1936); Iceland to English Channel (Schmidt, 1909).
Gadus callarius (Cod)	Spitsbergen to Bay of Biscay. Greenland to Cape Hatteras and Virginia (Sæmundsson, 1949; Hjort, 1912; Breder, 1948).	Barents Sea (Rass, 1936); northern Norway (Hjort, 1914; Wiborg, 1948); Iceland to English Channel (Schmidt, 1909).
Pleuronectes platessa (Plaice)	Barents Sea and White Sea to Portugal and Morocco; also recorded from northern parts of Mediterranean (Sæmundsson, 1949; Hjort, 1912; Schnakenbeck, 1929).	Barent Sea (Rass, 1936; Milinski, 1938); Iceland (Sæmundsson, 1949); North Sea to English Channel (Wallace. 1909).

Similar differences in the size-distribution of oocytes from various species have been noticed earlier, by investigators studying the fecundity of fishes (Fulton, 1891; Mitchell, 1913). These workers found it difficult or impossible to determine the fecundity of some species, because of the almost continuous gradation in cell-size between the large oocytes and the smallest cells at the spawning season. The latter are presumably follicle cells, or destined to provide the oocytes of later years. This is the condition found in *B. pholis*. In *C. gunnellus*, on the other hand, the uniformly large maturing oocytes can easily be distinguished from the much smaller yolkless cells, which will mature in subsequent years. There is therefore no difficulty in determining the fecundity of this fish. Similar conditions have been found in other northern fishes, such as plaice (Simpson, 1951), haddock (Raitt, 1933), cod (Fulton, 1891), and herring (Farran, 1938; Hickling, 1940).

Table 1 (continued).

Southern species (mediterranean-boreal)	Limits of Atlantic distribution	Known breeding range (European)
Blennius pholis (Shanny)	South-west Norway (Bergen) to Mediterranean (Duncker & Mohr, 1928; Ford, 1935; de Latil, 1954).	Non-migratory. As previous column.
Clupea pilchardus (Pilchard)	Southern Norwegian coasts to Mediterranean (Kyle & Ehrenbaum, 1927; D'Ancona, 1931).	North Sea (Furnestin, 1939); English Channel (Corbin, 1951); Bay of Biscay to Mediterranean (Fage, 1920).
Clupea sprattus (Sprat)	South-west Norway (Trondheim) to Mediterranean (Kyle & Ehrenbaum, 1927; Robertson, 1938).	South-west Norwegian coast (Mulicki, 1947); North Sea, English Channel, Bay of Biscay and Mediterranean (Fage, 1920; D'Ancona, 1931).
Gadus merlangus (Whiting)	Iceland to Mediterranean (Sæmundsson, 1949; Hjort, 1912; D'Ancona, 1933).	South of Iceland, North Sea, and other British waters to Bay of Biscay (Schmidt, 1909).
Merluccius merluccius (Hake)	Iceland to Mediterranean (Sæmundsson, 1949; Hjort, 1912; D'Ancona, 1933).	North Sea and other British waters to Bay of Biscay (Schmidt, 1909); Mediterranean (D'Ancona, 1933).
Scomber scombrus (Mackerel)	Iceland to Mediterranean. Labrador to Cape Hatteras (Sæmundsson, 1949; le Gall, 1932; Breder, 1948).	Southern Norwegian coasts (Dannevig, 1947); Swedish coasts (Nilsson, 1914); British waters (Allen, 1897); North Sea to Mediterranean (Ehrenbaum, 1924).

A correlation between the size frequency distribution of oocytes and the duration of the spawning season was first pointed out by Hickling and Rutenberg (1936). They showed that herring and haddock, which have short spawning seasons, have maturing oocytes all of approximately the same size, whereas pilchard and hake, which have long spawning seasons, have maturing oocytes of a wide range of sizes. These two conditions are also found in *C. gunnellus* and *B. pholis* respectively.

This difference between the breeding habits of *B. pholis* and *C. gunnellus* seemed at first to be rather surprising, for both species occupy a rather similar habitat (they may be found together under the same stone) and are fairly closely related systematically (both are placed in the Blenniiformes). The distribution of the two forms in other latitudes, however, is quite different. *B. pholis* is confined to the Atlantic coasts of Europe, from Bergen, in southern Norway (Duncker and Mohr, 1928; Ford, 1935), to the Mediterranean (de Latil, 1954). It therefore has its centre of distribution to the south of the British Isles. *C. gunnellus* on the other hand extends from Western Greenland, Iceland, and Norway to the English Channel (Sæmundsson, 1949). It is found on both sides of the Atlantic, like other arctic-boreal forms

from several phyla, and unlike mediterranean-boreal forms (Ekman, 1953). The lower sea temperature in the western Atlantic allows it to penetrate south as far as Massachusetts (Breder, 1948), but on the eastern side it has its centre of distribution to the north of the British Isles. It seemed probable that the differences observed between the breeding cycles of the two species were correlated with the fact that *B. pholis* is a southern form and *C. gunnellus* a northern form.

To test this hypothesis the breeding cycles of these species were compared with those of other marine teleosts of British waters, for which data are available (Tables 1 and 2). The species have been classified into northern and southern forms according to whether or not they have been recorded as breeding north of the arctic circle (Table 1). With the single exception of the plaice, the northern forms are found on both sides of the Atlantic. Of these forms the plaice appears to be the least adapted to cold conditions, for it alone extends to the Mediterranean, though it has not been found to breed there. Other migratory northern species, like herring, cod, and haddock, reach as far south as the Bay of Biscay in European waters, but *Centronotus gunnellus* and *Cottus scorpius* seem to reach their southern limits in the English Channel. The breeding range in all the northern forms seems to lie between the Arctic Ocean and the English Channel. Little is known about the breeding in extreme arctic regions, but is has been demonstrated in cod, by marking experiments, that mature individuals migrate during the breeding season, from polar regions to Iceland waters for spawning, and return to Greenland waters as spents (Hansen, Jensen, and Tåning, 1935).

The southern forms range mostly from the Mediterranean to the North Sea. Some of these species are also recorded from the south of Iceland and the Faroes during the summer, but they do not appear to breed in Icelandic waters, with the single exception of the whiting. The whiting seems to be less adapted to warm conditions than the others. The breeding range in most of these forms is from the Mediterranean to the northern parts of the North Sea, although the extreme northern limit of the breeding range varies in different species. The mackerel is found in American waters, as might be expected, since it is largely a fish of the open ocean. None of the other southern forms extends to the American side of the Atlantic.

Examination of Table 2 will show that all the southern species have breeding cycles similar to that of *B. pholis*, whilst all the northern species have cycles like that of *C. gunnellus*. The differences in breeding habits between the northern and southern groups may be summarized as follows:—

1. Southern forms spawn in late spring or summer, whereas northern forms spawn in late winter or early spring.

2. In southern forms the spawning seasons last for five or six months, but in northern forms they last only three or four months.

3. The maturing ovary of a southern species contains oocytes of a wide range of sizes, which are presumably destined to contribute to a

Table 2.

Fauna	Species	Size-range of oocytes in maturing ovary mm.	Time and duration of spawning in British waters (Dec. Jan. Feb. Mar. Apr. May Jun. Jul. Aug. Sep. Oct. Nov.)	Area investigated	Authors
Northern species (arctic-boreal)	*Centronotus gunnellus* (Gunnel)	0·84—1·10 (Present author)	+ + +	Irish Sea	Present author
	Clupea harengus (Herring)	1·11—1·26 (Farran, 1938)	+ + +	Southern North Sea	Hodgson, 1929
	Cottus scorpius (Sea scorpion)	1·20—1·27 (Fulton, 1891)	+ + + +	Irish Sea	Jenkins, 1936
	Gadus aeglefinus (Haddock)	1·20—1·39 (Fulton, 1891)	+ + + +	North Sea	Damas, 1909
	Gadus callarias (Cod)	1·20—1·40 (Fulton, 1891)	+ + +	North Sea	Graham, 1924
	Pleuronectes platessa (Plaice)	0·90—1·00 (Fulton, 1891)	+ + + +	North Sea	Buchanan-Wollaston, 1914
Southern species (mediterranean-boreal)	*Blennius pholis* (Shanny)	0·05—1·22 (Present author)	+ + + + +	Irish Sea	Present author
	Clupea pilchardus (Pilchard)	0·05—0·50 (Hickling & Rutenberg, 1936)	+ + + + + + +	Cornish waters	Hickling, 1945
	Clupea sprattus (Sprat)	0·06—1·12 (Fulton, 1891)	+ + + + + +	North Sea	Ehrenbaum, 1909 Tesch, 1909
	Gadus merlangus (Whiting)	0·05—1·30 (Fulton, 1891)	+ + + + +	Irish Sea	Bowers, 1954
	Merluccius merluccius (Hake)	0·05—0·50 (Hickling & Rutenberg, 1936)	+ + + + +	South and west of Ireland	Hickling, 1930
	Scomber scombrus (Mackerel)	0·05—0·90 (Fulton, 1891)	+ + + + +	Celtic Sea	Corbin, 1947

succession of spawnings. That of a northern species, on the other hand, contains oocytes which are all similar in size and which may therefore be spawned together. Evidence of spawning of individual fish more than once during a season has been obtained in several southern species, including the pilchard (Russell, 1930), the Californian sardine (Clark, 1934), the mackerel (Sette, 1943), the sprat (Heidrich, 1925), and *Blennius pholis* (present author).

Considering the adaptive significance of these differences between southern and northern forms, one thinks first of the well established fact that temperature is of great importance in controlling reproduction. This principle has been referred to by Thorson (1946) as Orton's rule, since it was first established by Orton (1920). Appellöf (1912) and others wrote of it earlier, but less precisely. Runnström (1927) dealt with it more recently. Amongst its corollaries is the rule that species which are nearer to the warmer limits of their range breed during the colder months of the year and, conversely, that species which are nearer to the colder limits of their range breed during the warmer months of the year. Such habits are of adaptive advantage, since the young are generally less tolerant of extreme conditions than are adults. Certainly newly hatched larvae of *C. gunnellus* are very sensitive to changes in temperature and soon die if the temperature rises above 12—13°C. Larvae of *B. pholis* can tolerate much higher temperatures. It may be presumed that northern fishes in British waters must breed very early in the year because their young larvae would be killed by the summer temperatures if they bred later.

There are several features of the breeding cycles of these fishes which are not fully explained by Orton's rule, however. We must still explain why the northern forms do not breed over a long period during the colder months of the year and why the southern forms do not go on breeding in autumn, when the water is at its warmest. We may consider why *C. gunnellus* in Iceland, as in British waters, breeds for only two or three months at the coldest time of the year (Sæmundsson, 1949). Turning to another group of animals, the barnacles, which resemble fishes in having a long embryonic stage in the development, followed by a planktotrophic larval stage, we again find several features of the breeding cycles which are not easily explained on the basis of Orton's rule alone. As in fishes, the southern barnacles, which breed in summer, produce a succession of spawnings over a long period of several months (Crisp, 1950; Crisp and Davies, 1955) whereas the northern forms, which breed in winter, spawn during a shorter period, each individual producing a single brood annually (Crisp, 1954). The common arctic-boreal shore barnacle, *Balanus balanoides*, which is at its southern limit in the English Channel, spawns in British waters during November (Moore, 1935), which is far from being the coldest season of the year. The embryonic development goes on within the mantle cavity of the parents until the spring, when the planktotrophic larvae are liberated. At higher latitudes the embryos are still retained throughout the coldest months, so that they are liberated in

the spring when conditions are favourable for feeding and growth of the larvae (Crisp, 1954).

This behaviour suggests a principle that may be generally applicable to the breeding cycles of marine animals which have planktotrophic larvae. The breeding cycles may be so regulated that the larvae hatch during the season which is most favourable for finding planktonic food, under the conditions that prevail over the greater part of their range. I should like to refer to this as Crisp's rule, since it was suggested to me by Dr. D. J. Crisp, who has deduced it from his work on the breeding of barnacles. We have here an explanation of why *C. gunnellus*, in Iceland, breeds so early in the year, and why breeding seasons are short in northern fishes. In higher latitudes organic production in the plankton is restricted to a short period during early summer, when it is intense (Steemann Nielsen, 1935; Jespersen, 1940). The planktotrophic larval stage must occur during this period, so the fish must spawn much earlier, since at low temperatures spawning is separated from hatching by a fairly long phase of embryonic development. At the spawning season temperatures and food supply are at about their annual minimum, so presumably conditions of life, for the adult fish, are too poor to support the maturation of successive batches of eggs. Each fish therefore puts all its reserves into one batch. The eggs of northern fishes seem to be generally larger than those of southern forms, as in many invertebrates (Thorson, 1950). Hence the hatching larvae are probably well supplied with yolk, which will maintain them for a time if they should have difficulty in finding food.

In middle latitudes plankton production goes on at moderate levels throughout the spring and summer. But northern forms, even in these warmer parts of their range, must continue to breed in winter or early spring to provide optimum conditions for their stenothermal young. Hence, even in these milder climates, their breeding cannot occur at a season when abundant food for the parents would favour a succession of broods.

In low latitudes plankton production is said to go on at a comparatively low level throughout the year. Optimum conditions must be affected by the weather and may therefore occur at almost any time. Southern species, by spawning at intervals, ensure that larvae are present in the plankton over a long period, ready to take advantage of optimum conditions whenever these occur. Conditions are favourable for the building up of reserves by the adult fish during the spawning season, so each female brings to maturation successive batches of eggs. In southern species, which guard the eggs during an incubation period, this duty is always performed by the males. Well known examples are *Blennius pholis*, *Blennius ocellaris* (Lebour, 1927), *Blennius gattorugine* (Brown, 1929; Wilson, 1949), *Blennius sphynx*, *Blennius montagui*, *Clinus argentatus* (Guitel, 1893), and *Gobius minutus* and other gobies (Jenkins, 1936). The females are therefore left free to take advantage of abundant food, and their successive batches of eggs may be added to the previously laid masses, as in *Blennius pholis*. In

northern forms which breed only once in the season, during winter, when conditions for the building up of reserves are not very favourable, it is immaterial which of the sexes guards the eggs. In such forms we find this duty taken up by females, as in the crested blenny (Schultz and De Lacy, 1932), or by males, as in *Cottus scorpius* (Ehrenbaum, 1904), or by both sexes, as in *Centronotus gunnellus* (Gudger, 1927).

In British waters, spawning of southern forms generally finishes before September (Table 2). The young therefore have a growth period of at least two or three months before the sea becomes really cold. In *B. pholis* the gonads recover remarkably quickly after spawning and remain large during the winter. This rapid recovery also occurs in hake (Hickling, 1930) and whiting (Bowers, 1954). It is probably a feature characteristic of southern forms living in boreal waters, which enables them to take advantage of the warmth and food still available to them in the autumn.

Crisp's rule (in conjunction with Orton's rule, for fish larvae are undoubtedly more stenothermal than adults) therefore provides a complete explanation for these differences between the breeding cycles of southern and northern fishes, in terms of adaptive advantage to the species. But the problems of which point in the cycle is linked to the cycle of the seasons, and of whether the link is to temperature, to length of day, or to some other factor, remain to be solved by future experiments.

I am grateful to Dr. E. W. Knight-Jones for suggesting this problem to me, kindly reading through the manuscript of the paper, and offering valuable suggestions for its improvement. I am also much indebted to Mr. A. C. Simpson, of the Fisheries Experiment Station, Conway, for some important references, and help and criticism in the preparation of the paper.

Summary.

The breeding cycles of marine teleosts in British waters are governed by the following general principles:—

1. Northern (arctic-boreal) forms breed during winter or early spring, and southern (mediterranean-boreal) forms during spring and summer.

2. The breeding of northern forms lasts for only three or four months, but that of southern forms lasts for five or six months.

3. In northern forms the maturing oocytes are all of similar size and the eggs are probably spawned in a single group. Southern forms have maturing oocytes of a wide range of sizes, destined to be matured and shed periodically.

It is suggested that the breeding cycles of all these forms are adapted to provide optimum conditions of food and temperature for the larvae. During the warm breeding seasons of southern forms, moreover, sufficient food is available for the adults to support the maturation of

successive batches of eggs. Northern forms, on the other hand, spawn at a season which is not very favourable for feeding, so the females put all their reserves into a single batch.

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Chemical Composition of the Zones in Cod Otoliths.

By

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IT is of the greatest importance to the marine biologist to be able to determine the age of a fish with accuracy. In most cases this can be simply done by counting the rings of growth in the otoliths.

In the course of a year two rings, or zones, are formed in the otolith; one opaque zone (see Figure 1), which appears dark in the diagram (in transmitted light), and one transparent zone, which appears light. The transparent zone in the otoliths of cod caught near the Norwegian coast is formed during the months August—November (the "summer" season in the intermediate layers of the sea), while the opaque zone develops between December and July (D a n n e v i g, 1933). Thus these growth rings are formed periodically, and can be used to determine the age of the fish. The problem of the factors that affect zone formation and produce the differences between the transparent and the opaque zones is one which has occupied the attention of scientists for more than a century.

In this paper only the last part of the problem, the composition of the different zones, is dealt with. It may be mentioned, however, that analyses of the different body fluids are being made to determine what changes take place during the year, since there may perhaps be some correlation between the formation of zones in the otoliths and the composition of the body fluids. The results of these investigations will be published later. Experiments are also being undertaken to determine whether zone formation is affected by external factors, or whether it is merely a result of the life cycle, and more or less independent of ecological factors.

One of the earliest investigators in this field (K r i e g e r, 1840) came to the conclusion that the zones resulted from differences in the density of the crystals of which the otolith consists. R e i b i s c h (1889), who worked with otoliths from *Pleuronectes platessa,* found, however,

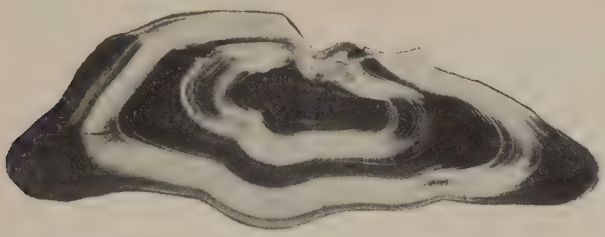

Figure 1. Cod otolith as seen by transmitted light.

that the zones were formed from organic material that was present in layers alternating with layers of pure amorphous calcium oxide. He also assumed that zone formation was dependent on water temperature, the transparent zone (which he believed to be pure amorphous calcium oxide) arising in warm water (in the summer), and the opaque zone (containing organic material and less calcium oxide) developing in colder water (in winter). Jenkins (1902), who analysed otoliths from the Clupeidae, found, on the other hand, that the zones were formed from amorphous calcium oxide that had been precipitated in layers between layers containing pure organic material.

Dr. Gulbrand Lunde (1929) made some complete analyses of the inorganic material in otoliths from cod (spawners from the Flødevigen Sea-Fish Hatchery). His results are summarized below:—

	%
FeO	0·0026
MnO	0·007
MgO	0·07
CaO	54·24
CO_2	33·59
Na_2O	0·44
K_2O	0·09
P_2O_5	0·11
SO_3	0·019
Cl	0·003
H_2O (—110°C.)	0·22
H_2O (+110°C.) + organic substance	11·27
	100·0616

According to this analysis, it would appear that the main substance present in the cod otolith is calcium carbonate. There is, however, not enough CO_2 present to combine with all the CaO, so some of this must therefore occur as oxide. This is verified by the fact that a pulverized otolith reacts as alkaline in water.

The cod otolith may therefore be regarded as consisting of:—

	%
$CaCO_3$	76·39
CaO	11·44
H_2O + organic material	11·49
Other compounds	0·68
	100·00

An X-ray examination (with pulverized otoliths) showed the calcium carbonate to be present only as aragonite. Furthermore, it also proved that no other crystalline compound was present in the cod otolith, since the diagram exhibited no lines other than those originating from aragonite.

The cod otolith thus consists of calcium carbonate (aragonite), with some calcium oxide and organic material. To this extent the composition of the otoliths may be regarded as established. However, in connexion with some other work being conducted on cod, it was necessary to determine the factors which influence zone formation, and the changes which take place during the formation of the different zones. As a first step in that direction the composition of the organic material was examined, together with the chemical differences between the transparent and the opaque zones.

If an otolith is broken in two and heated in a Bunsen burner, the zones containing organic material turn black, while the rest is unchanged. It can be demonstrated in this way that the organic material is located in the centre of the otolith and in the opaque zones, whereas the transparent zones contain only inorganic material. By careful decalcination, with chromic acid, of thin sections of the otoliths, all the inorganic material is dissolved, but some membrane-like material will remain. This residue occurs where the opaque zones were located, and is evidently part of them.

The presence of these membranes can also be shown by careful decalcination of the whole otolith in dilute acid. After the liberation of CO_2 has ceased, a membrane can be observed surrounding the whole otolith like a cellophane wrapping. If this membrane is ruptured, or removed, the dissolution of the otolith starts again and continues until a fresh membrane is reached. There is one membrane for every second ring of growth.

The centre contains relatively more organic material than does the rest of the otolith, as is demonstrated by analyses of otoliths of different sizes. Large otoliths were found to contain 54·86 % CaO, and small otoliths (from cod caught in the same localities as the large ones) only 52·5 % CaO.

The organic material is a protein, a conchiolin, closely related to the organic material in the shell of certain molluscs (B e e d h a m, 1954). It is insoluble in weak acids and alkalis, but hydrolyses in strong. It gives positive Biuret and xanthoprotein reactions. Untreated conchiolin

does not, however, give any colour reaction with ninhydrin, and accordingly does not contain a free α-amino-acid group.

When chromatograms are run on conchiolin hydrolysed for 24 hours at 110°C. with 6 N HCl, spots representing 14 or 15 different amino-acids occur on the chromatogram. These amino-acids, which linked together form the conchiolin, are (see Figure 2):— lysine, asparagine, arginine, serine, glycine, glutamic acid, threonine, alanine, proline, valine, phenylalanine, leucine + isoleucine, and taurine.

The solvents used were:— n-butanol : acetic acid : water and phenol : water in an NH_3 atmosphere. The amino-acids were identified by means of known standards.

The organic material present in the cod otoliths could not be separated into more than this fraction, and conchiolin may therefore be regarded as the only substance present.

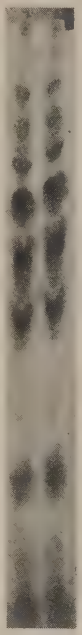

Figure 2. Chromatogram of hydrolysed conchiolin from cod otoliths.

Summary.

A complete analysis of the inorganic and organic material in cod otoliths shows their composition to be 76·39 % $CaCO_3$ (aragonite), 11·44 % CaO, 11·49 % H_2O + organic material, and 0·68 % other compounds. The organic material is a protein, conchiolin. Its amino-acid constituents are given. The calcium compounds are deposited in all parts of the otolith. The transparent zone (formed in the marine "summer") contains inorganic compounds only, and the opaque zone (formed in "winter") contains both calcium compounds and conchiolin.

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The "Critical Period" in the Early Life History of Marine Fishes.

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Introduction.

Postulation of the existence of a "critical period" (of high mortality rate) during the early life history of those marine fishes which are extremely fecund was ably dwelt upon forty years ago by Hjort (1914). This idea has been rather generally accepted, if not as fact, at least as a very reasonable hypothesis; it has had a profound effect upon marine fishery biology.

The implications of this hypothesis are rather far-reaching and it is therefore pertinent to briefly review the hypothesis, to consider the form that early survival curves may take, and to contemplate the accumulated evidence bearing on whether or not there is in fact such a "critical period" *in nature*.

The hypothesis.

Hjort (1914: 203) stated: "The rich year classes [of fishes] thus appear to make their presence felt when still quite young; in other words, the numerical value of a year class is apparently stated at a very early age, and continues in approximately the same relation to that of other year classes throughout the life of the individuals." And (p. 204): "We must therefore look to the later stages of the eggs to find the conditions which determine the numbers of individuals in any year class. This again leads us to the question, at which stage of development the most critical period is to be sought. Nothing is known with certainty as to this; such data as are available, however, appear to indicate the very earliest larval and young fry stages as most important."

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He also suggested two possible methods by which such early reduction in numbers might be accomplished, and subsequently (Hjort, 1926: 33) re-stated these as:—

"1. That those individuals which at the very moment of their being hatched did not succeed in finding the very special food they wanted would die from hunger. That in other words the origin of a rich year-class would require the contemporary hatching of the eggs and the development of the special sorts of plants or nauplii which the newly hatched larva needed for its nourishment.

2. That the young larvae might be carried far away out over the great depths of the Norwegian Sea, where they would not be able to return and reach the bottom on the Continental shelf before the plankton in the waters died out during the autumn months of their first year of life."

Following Hjort's hypothesis, and in spite of a notable paucity of observational or experimental data, fishery biologists have come to accept it as almost axiomatic that year-class size of marine fishes is determined during the first few days or, at most, months, of life. (There is, however, a large group of fishery biologists who assume, again in spite of a lack of data, that year-class size is determined even before the eggs are spawned; i.e., that it is a function of stock size. This assumption does not require that there be or be not a critical period. But it does require that the net survival rate either be constant in all years or that it be some function of stock size, so that the number of eggs spawned determines the size of the resulting year-class.)

At least three different life-history stages have been suggested as the one which is most critical. Rollefsen (1930) has suggested that cod (*Gadus callarias*) year-class size is determined in the egg stage, according to whether or not the eggs are damaged by wave action. Hjort (1926) has, as already noted, suggested that the time of yolk absorption is critical, success or failure of the year-class depending on an abundant food supply when the larvae commence feeding. Hjort (1926) and Sund (1924) have suggested that the larval stages may be most critical, depending on the influence of the currents on the distribution of the larvae to favourable or unfavourable locations.

Even earlier, Fabre-Domergue and Biétrix (1897), who were interested primarily in marine fish culture, had observed high larval mortality rates in rearing trials occurring at about the time of the completion of yolk absorption. To this phenomenon they applied, for the first time, the term "la période critique". Since that time references to this critical period are common in the works of marine fish culturists and, more recently, in the works of those attempting to rear marine fishes for experimental purposes (see, for example, Morris, MS).

It is obvious, as Hjort reasoned, that in species which spawn large numbers of eggs, there must be a tremendous mortality sometime between the time the eggs are spawned and the time at which the fish assume the adult form and habit. For example, the size of the spawning

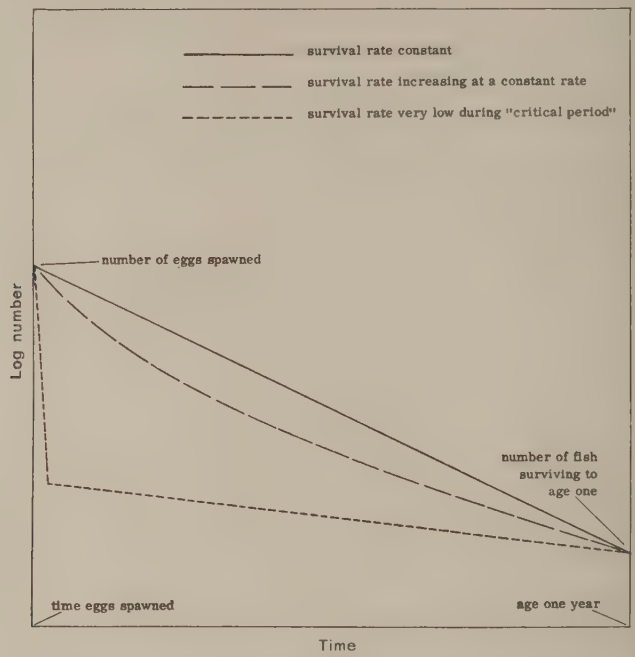

Figure 1. Three forms (schematic) which fish survival curves could take, from the time the eggs are spawned to age one year.

stock of the Pacific sardine (*Sardinops caerulea*) in 1942 was $7{\cdot}6 \times 10^9$ fish (this is a minimal estimate, based on fish actually caught, and does not take into account deaths from natural mortality; see Clark and Marr, 1955). According to Clark (1934) each female sardine (of the length common in the population then) would have spawned, on the average, about 100,000 eggs per year. The 1942 stock must therefore have spawned about $3{\cdot}8 \times 10^{14}$ eggs. A minimal estimate of the 1942-class, which resulted from these eggs, is $2{\cdot}3 \times 10^9$ fish at age two years, or a reduction to 0·000605 % of the original number in two years' time. Similar examples may be found in all species for which the appropriate data are available.

Form of early survival curves.

While the reduction in population numbers from eggs to, say, age one year is obvious, it is difficult and costly to make observations on the nature of this reduction and the time at which it occurs. As a consequence, data on early mortality or survival rates in the sea have been collected for only a few species. Before considering these data, it is pertinent to consider the form that early survival curves might be expected to take.

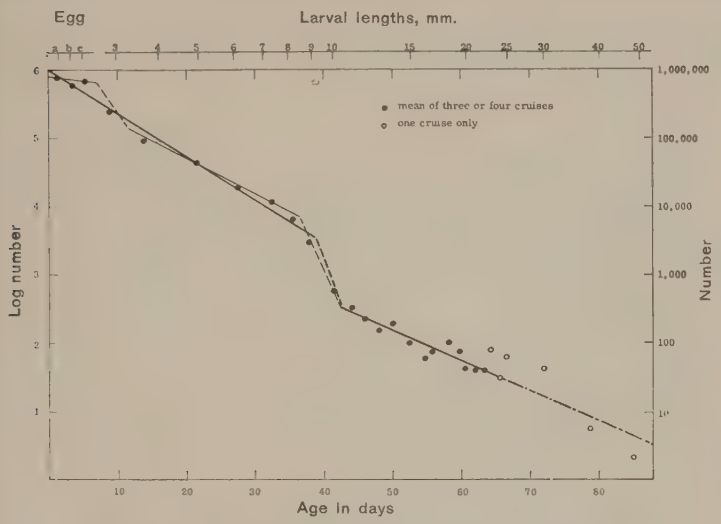

Figure 2. Survival of young stages of Atlantic mackerel. (From Sette, 1943, Figure 17.)

Three such hypothetical survival curves are shown in Figure 1, in which the logarithms of the numbers of fish are plotted as a function of time. The curves start with the number of eggs spawned and represent three different types of survival to age one year. The number of eggs spawned and the numbers of fish surviving to age one year are the same in each example.

The "critical period" type of survival curve is shown by the dashed line. This curve is characterized by an extremely low survival rate (or high mortality rate) during the early "critical period". In the hypothetical example given, a constant survival rate is shown following the "critical period", but this portion of the curve could, of course, be of some other form. In survival of this type, it is usually hypothesized that the extent of mortality during the "critical period" is the dominant factor in determining the numbers surviving to age one.

A second type of survival curve, in which the survival rate is increasing at a constant rate, is shown by the broken line. Even though, as in the "critical period" curve, mortality rate is greatest at the earlier stages, it is the survival rate over the whole period which determines the numbers surviving to age one.

The third hypothetical curve, shown by the solid line, represents a constant survival rate over the entire period. In this type of survival the numbers surviving to age one are, obviously, determined by the constant survival rate.

All of these curves are idealized beyond what one would expect to observe in nature. Furthermore, it would be possible for survival to

follow some combination of these hypothetical curves, or some completely different curve. For example, the survival rate might decrease at a constant rate, although this does not seem likely.

The evidence.

The first work that I have been able to find which deals critically with the early survival rate of marine fish is that of Sette (1943) on the Atlantic mackerel (*Scomber scombrus*) of North America. He gives a survival curve of the 1932-class over the first 85 days of life, during which period the larvae attain a length of about 50 mm. His Figure 17 is reproduced here as my Figure 2. A thorough discussion is given by Sette (1943: 191—208) of the derivation, reliability, possible sources of error, and significance of this survival curve.

Pertinent to this discussion is the slope of the curve. Of the two possible interpretations of the data given by Sette, both are characterized by a period of high mortality at age 40 days or larval length of 9—10 mm. One interpretation involves a uniform survival rate up to age 40 days, the alternative involves three different rates during this period. In neither case is the mortality rate such that it could be considered to constitute a "critical period" at the time of yolk absorption. Indeed, as Sette (1943: 203) stated: "If any one period is to be singled out as the most critical, it must be the ensuing period during the transition from larval to post-larval stages, when in passing from 9 to 11 mm., the numbers are reduced by 90 percent in the short space of about 3 days." And (1943: 204) "... one may say that about one-third of the mortality was suffered during the so-called 'critical' stages, and the other two-thirds during what might be called 'non-critical' stages."

The change in the estimated survival curve at larval size 9—10 mm. may arise from one of three causes; (1) it may actually represent a period of high mortality, (2) it may represent a period when the larvae are not caught in proportion to their true abundance (either because of increased swimming and net-dodging ability or because some of them have moved out, horizontally or vertically, of the water sampled by the nets), or (3) it may represent a temporary period of reduced rate of growth. Some evidence for increased dodging ability is found in the fact that at larval size 9—10 mm. great changes occur in the fins. In fact, Sette (1943: 171) characterizes this as the "transition phase" and states that "... the tail fin makes its greatest changes, the second dorsal fin and finlets and the anal fin and finlets are all developed within this size range ..."

However, he concluded that larval sizes up to 22 mm. were sampled in proportion to their true abundance, on the basis of catches of 1- and 2-m. nets hauled at the same stations. That is, the 1-m. net took larvae in about the same numbers as did the 2-m. net, per volume of water strained. This would not necessarily rule out the possibility of dodging, however, if the maximum size net which the larvae were able to dodge was greater than 2 m.

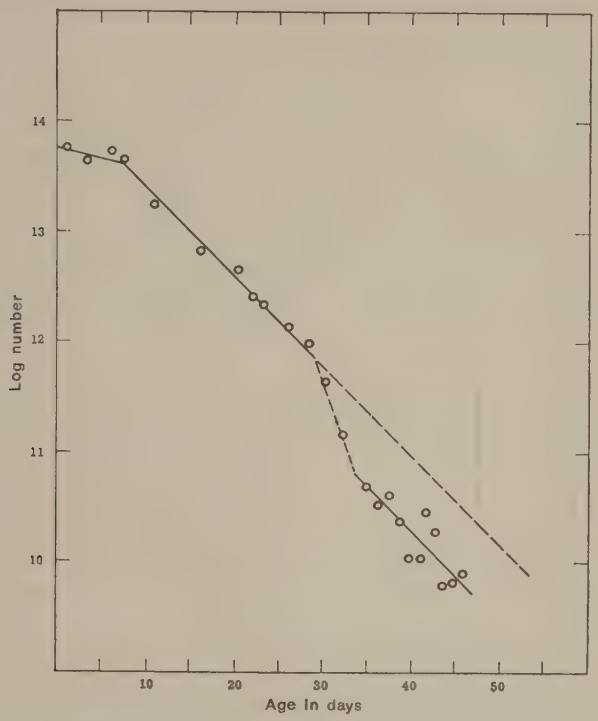

Figure 3. Survival of young stages of Atlantic mackerel. (From Ahlstrom & Nair, MS, Figure 7.)

Ahlstrom and Nair (MS) have recently re-examined Sette's data. Their analysis differs from his in that they take into account (1) the distribution of eggs and larvae in space and time and (2) the differences between day and night catches, and (3) they have also re-determined larval growth-rate. Their Figure 7 is reproduced here as my Figure 3. Even with these added refinements of analysis, it is apparent that so far as this discussion is concerned, the main features of the estimated survival curve remain the same. Two features are of interest, however. The new estimate supports one of Sette's alternatives, namely, that mortality rates are less for eggs than they are for larvae. This could not be considered a "critical period" in the accepted sense of that term. The apparent short period of low survival rate (which now occurs at about age 31 days owing to the recalculation of growth-rate) is followed by a rate which is similar or identical to that of the earlier period. This lends additional credence to the possibility that the abrupt change in survival rate is not real, but represents increased net-dodging ability after fin formation. The growth data do

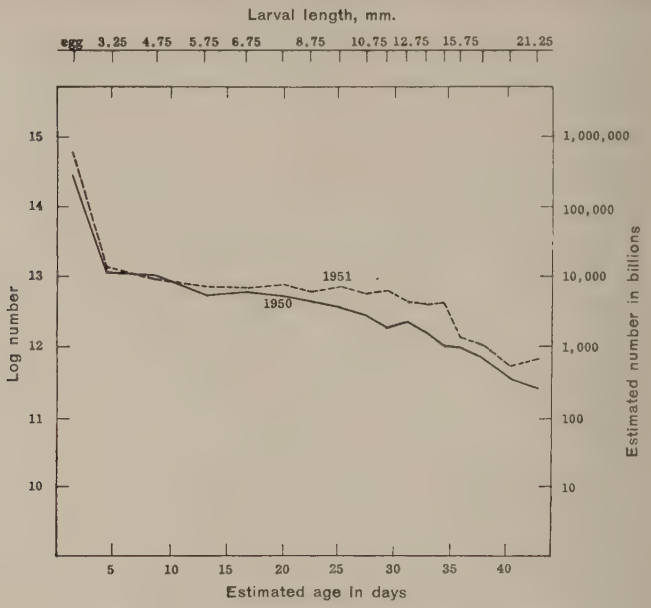

Figure 4. Survival of young stages of Pacific sardine in 1950 and 1951.
(From Ahlstrom, 1954, Figure 31.)

not show a reduced growth-rate in 9—11 mm. larvae (see Figure 5, Ahlstrom and Nair, MS). It is not now possible to make a final choice between the other two possibilities (dodging or mortality); this must be based upon additional observations at sea.

The second study which deals critically with the early survival of a marine fish is that of Sette and Ahlstrom (1948) and Ahlstrom (1954) on the Pacific sardine (*Sardinops caerulea*) of North America. The latter has given survival curves of the 1950- and 1951-classes over the first 45 days of life, during which the larvae attain a length of 21·25 mm. His Figure 31 is reproduced here as my Figure 4. The survival curve of the 1952-class (unpublished data) does not differ in general form from those for the 1950- and 1951-classes.

These curves lead one to infer a high mortality rate between the eggs and the 3·25 mm. larvae, a very low mortality rate between the 3·25 and 14·75 mm. larvae, and a higher mortality rate for larvae larger than 14·75 mm. The yolk-sac of sardine larvae is absorbed by about 4·50 mm. and these curves, therefore, might well be interpreted as exhibiting an early "critical period". However, as Ahlstrom (1954: 56—72) points out, some of the newly hatched larvae are lost through the meshes of the plankton nets. Such loss decreases as the larvae increase in size. While the exact amount of these losses has not yet been determined, present evidence (unpublished) indicates that, for

example, only about one-tenth of the 3·25 mm. larvae that enter the net are retained by it. This suggests that the true shape of these survival curves is such that the survival rate increases at a nearly constant rate, as shown by the broken line in Figure 1.

The terminal increase in mortality rate in the sardine survival curves may be real or it may only represent undersampling, such as would be caused by net-dodging by the larger larvae. Only additional observations will indicate which is the correct alternative.

I have been unable to find any other published studies of the early survival of marine fishes which are as comprehensive as those of the Atlantic mackerel and the Pacific sardine. Mr. D. A. Farris, U. S. Fish and Wildlife Service, has in progress a similar study of recent year-classes of the jack mackerel (*Trachurus symmetricus*), but this is not yet sufficiently advanced to estimate the form of the early survival curve.

Mr. A. C. Simpson, Ministry of Agriculture and Fisheries, England, has started a similar study of the plaice (*Pleuronectes platessa*), which has not yet been published. However, he has kindly informed me (personal communication dated 22. January 1954) that in the first year of surveys "... there was no evidence that pointed to a catastrophic mortality at any stage".

Soleim (1940, 1942) has inferred that herring have a "critical period" which coincides with the time of yolk-sac absorption and is the result of a lack of sufficient food. (These papers are in Norwegian; I have been able to read only the English summaries and an English translation of the 1942 paper which is in the library of the International Fisheries Commission, Seattle.) He bases this inference on three sets of observations:— (1) The numbers of larvae taken in plankton hauls (off the coast of Norway) decrease rapidly with increase in length of larvae. (2) Some of the plankton hauls contained, in addition to larvae which had obviously been alive when caught, large numbers of larvae which had obviously been dead some time before capture. These larvae were largely at the stage of yolk-sac absorption. (3) In rearing experiments in the laboratory, large numbers of larvae died following yolk-sac absorption.

The latter need not be considered here, since I am concerned only with the existence of a "critical period" in nature. With reference to (1) above, "numbers as a function of size" survival curves may be misleading as compared to the true "numbers as a function of age" survival curves, since at different sizes of larvae a unit increase in size represents different time periods. But there exists an even more serious objection to Soleim's inference. Unless the area of spawning and area of larval drift are adequately encompassed in time and space, variations arising from sampling deficiencies may appear in the survival curves. Without additional data it will be impossible to ascribe the exact cause of such variations. It is not apparent that the area was adequately encompassed in space and time.

Concerning (2) above, dead larvae taken in plankton hauls may

have starved to death, but, alternatively, they may have died as the result of bacterial infection, or any of a number of other causes. Furthermore, the appearance of dead and disintegrating larvae in plankton collections may simply be an artifact. Such larvae are common, for example, in hauls which also contain large numbers of hard, sharp forms, such as pteropods. Damage to the larvae obviously results from contact with the pteropods within the plankton net. A more common source of dead larvae in a given plankton haul is contamination from the previous haul; i.e., inadequate washing of the net between hauls. This appears to be the most likely explanation of the appearance of dead herring in S o l e i m' s hauls. According to his Table 1 (1942: 8), the hauls in which large numbers of dead larvae occurred invariably followed hauls in which large numbers of normal larvae were taken. Dr. E. H. A h l s t r o m has informed me (personal communication) that in our studies of the Pacific sardine and other pelagic species, the occurrence of dead larvae in plankton collections always follows inadequate washing of the net between hauls.

Pending additional information, I conclude that this record of dead herring larvae probably represents an artifact. However, the possibility that they died before capture, of starvation or some other cause, is not completely eliminated. For example, dead newly hatched jack mackerel larvae were taken off the coast of southern California at 30°58·5′N. Lat., 120°45′W. Long. on 24. March 1954. In a day-time series of vertically stratified horizontal hauls, jack mackerel larvae were taken at 7 levels from the surface to 67·5 m. The surface haul (0903—0913 PST) contained 73 newly hatched larvae, of which 69 were in a disintegrating condition with missing heads. The haul of 6·8 m. (0935—0946 PST) contained 76 larvae, of which 70 were dead. All other jack mackerel larvae captured at greater depths were of normal appearance. In a similar night-time series, jack mackerel larvae were taken at 5 levels from the surface to 64·2 m. The surface haul (2025—2035 PST) contained 11 newly hatched larvae, of which all were dead. Jack mackerel larvae were absent in the 6·8 m. haul, but 3 in normal condition were taken in the 17·4 m. haul (2120—2130 PST). The cause of this mortality is not known. It was not an artifact arising from inadequate washing of the net between hauls because (1) the net was new and had never been used before the first surface haul and (2) dead larvae were not found in the hauls between the day and night surface hauls. Neither was it the result of thermal stratification at the surface, since during the day series the temperature was 14·1°C. at the surface and 14·0°C. at the 53·2 m. level; during the night series it was 14·3°C. at the surface and 14·1°C. at the 64·2 m. level.

In addition to the Atlantic mackerel, sardine, herring, and jack mackerel data discussed above, there are, scattered through the literature, data (on various species) which are almost, but not quite, suitable for the derivation of survival rates. An example is the information on coalfish (*Gadus virens*) given by B e r t e l s e n (1942). Even though such contributions were not intended to bear on this subject, one cannot help but wish that they were.

Summary and Conclusions.

Although the "critical period" hypothesis of the cause of fluctuations in year-class sizes of marine fishes was postulated forty years ago, little evidence with which to test the hypothesis has been accumulated since then.

Of the various forms which early survival curves could take, three seem most likely to obtain. These are (1) the "critical period" type, with catastrophic mortalities restricted to a brief period, (2) the form in which the survival rate is increasing at a constant rate, and (3) the form in which survival rate is constant.

Data with which these possibilities may be examined have been published for only one year-class of Atlantic mackerel and two year-classes of Pacific sardine. The Atlantic mackerel data may be interpreted as having relatively constant survival rate, but with a brief period of high mortality (which may be real or may be the result of increased swimming ability of the larvae) at about age 30—40 days. There is no "critical period" at the time of yolk absorption. The Pacific sardine data may be interpreted as having an early "critical period" of high mortality. However, only about one in ten of the smallest larvae were retained by the nets used and it is likely that the true survival rate is increasing at a constant rate.

Records of the natural occurrence of dead larvae may be real or may be artifacts.

The question "Is there a 'critical period' *in nature* in the early life history of marine fishes?" cannot yet be answered categorically. Catastrophic mortalities restricted in time will always remain as a possibility, of course, but the weight of what little evidence there is points toward survival at a constant rate or at a constantly increasing rate, rather than toward the existence of a "critical period".

I have tried to explore the implications of these two general types of mortality (one concentrated in time and the other spread over a longer period) on the hypotheses which biologists will wish to test and, especially, on the methods of testing them. In either case the causes of mortality may be the same. However, in the case where mortalities are severely restricted in time, one might expect that the causes would be more striking or obvious and thus be more readily recognized. Yet, if the mortalities are severely restricted in time, even though obvious, the chances that the observer will make the right observations at the right time and the right place are greatly reduced. If, on the contrary, the mortalities are spread over a longer time, one might expect that the causes would be less striking and not so readily recognized. But the observer will have better chances of making the right observations at the right time and place.

Acknowledgements.

I wish to thank E. H. Ahlstrom, O. E. Sette, and T. M. Widrig, U. S. Fish and Wildlife Service, and A. C. Simpson,

Ministry of Agriculture and Fisheries, England, for critically reading and commenting upon this paper, and George Mattson, U. S. Fish and Wildlife Service, for preparing the figures.

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Über das Eingeweidefett ("Ister") des Herings.

Von

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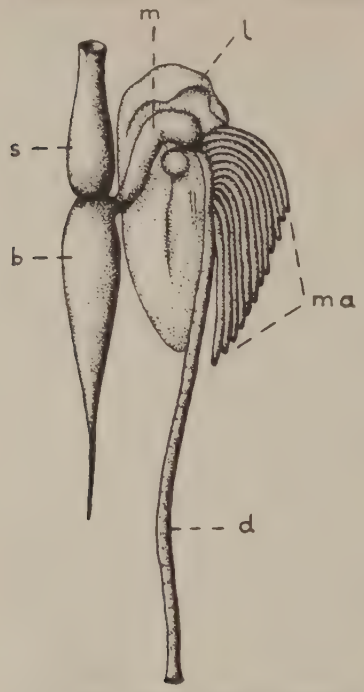
BEI den Analysen frischer Heringe auf See an Bord von Loggern und Fischdampfern im Rahmen des Heringsuntersuchungsprogramms des Instituts für Seefischerei in Hamburg wurden seit Juni 1953 Aufzeichnungen über den Entwicklungszustand des Fettgewebes in der Leibeshöhle gemacht. Damit sollte nicht nur der Fettgehalt — ihre Qualität nach der Definition von H j o r t (Rapp. et Proc.-Verb., **20**, p. 168, 1914) — festgestellt werden, sondern auch Anhaltspunkte dafür gewonnen werden, zu welchem Zeitpunkt die einzelnen Heringe ihren Laich abgelagt hatten (B j e r k a n, Rep. Norw. Fish. Mar. Invest., **3**, 1, p. 26, 1917), also zu welchen Laichstämmen sie gehören.

Die ganz jungen Heringe zeigen noch keine Fettansammlungen. Von bestimmter Länge an erfolgt deren Ausbildung (Reifestadium I). Dann füllt sich allmählich die ganze Leibeshöhle mit weissem, sehr zartem und leicht verletzlichem Fettgewebe, dessen Gliederung am besten nach Konservierung mit aufgeschnittener Leibeshöhle festgestellt werden kann. Der Verdauungstraktus des Herings (Fig. 1) ist bei der höchsten Fettausbildung ganz in Fett eingebettet, und man kann folgende Komponenten des Gewebes unterscheiden:—

1) Vom Oesophagus an ist das nach hinten gerichtete Caecum vollständig von prallem Fettgewebe umschlossen, das in einem spitz zulaufenden Lappen noch weit kaudalwärts reicht.
2) Der an dem Blindsack ansetzende starkwandige Muskelmagen trägt keinen Fettansatz.
3) Die Pylorusanhänge sind so dicht von Fettgewebe umwachsen, dass sie unter Einschluss des Muskelmagens als ein grosser Fettklumpen erscheinen.



Figur 1. Darmtraktus des Herings. (Alimentary canal of the herring).

s = Oesophagus
b = Caecum
m = Muskelmagen (muscular stomach)
ma = Pylorusanhänge (pyloric appendages)
l = Leber mit Gallenblase (liver and gall bladder)
d = Darm (intestine)

Milz und Pankreas sind fortgelassen (milt and pancreas are omitted).

(Nach Lissner)

4) Der Darm trägt in seiner ganzen Länge an beiden Seiten je ein Band von Fettgewebe, das besonders in seinem Anfangs- und Endteil vielfach stark verdickt ist.
5) Im innersten Teil der Leibeshöhle liegt beiderseits der Mittellinie ihrer Auskleidung auf einer dünnen Muskelschicht von der Schwimmblase ab je ein nicht sehr starker Fettsreifen, der kaudalwärts spitz ausläuft und auf dessen hinterem Teil die noch sehr dünnen Gonaden aufliegen.

Dies ganze Fettgewebe wird mit zunehmender Entwicklung der Gonaden abgebaut, sodass von Reifestadium IV—V die Leibeshöhle statt mit Fettgewebe ganz von den Gonaden ausgefüllt ist.

Bei der Analyse der Heringsproben von je 100 Stück auf See wurden ähnlich wie bei den früheren Untersuchungen (die mir übrigens erst später bekannt wurden) 4 Stadien unterschieden:—

Ausgezeichnet (4): Die Leibeshöhle ist ganz oder fast ganz von breiten Fettlappen und -bändern erfüllt.
Sehr fett (3): Weniger Fettgewebe, Leibeshöhle etwa halb voll, doch noch reichlich Fettlappen und breite Darmbänder.
Fett (2): Etwa bis $^1/_4$ voll, die Darmbänder sind viel weniger breit.

Kaum fett (1): Kein Fettgewebe bis auf sehr schmale oder nur angedeutete Darmbänder oder auch diese nicht mehr zu erkennen.

Durch Umrechnung kann man für jeden Fang auf Grund der Analyse von 100 Heringen einen "Fett-Index" erhalten, indem man die Anzahl der Heringe der einzelnen Fettgruppen je mit der Bewertungsziffer multipliziert und die erhaltenen Werte addiert. Die Analysen der Fänge können somit vom besten bis zum schlechtesten Fang alle Indices zwischen 4·00 und 1·00 ergeben. Übrigens liegen die so erhaltenen "Fett-Indices" um 1·00 höher als die Fettwerte von Bjerkan, da seine 0-Werte unberücksichtigt blieben.

Vergleicht man die Index-Werte mit den Geschlechtsreifebestimmungen, so ergibt sich über die Fettabnahme mit zunehmender Geschlechtsreife:—

Reife	Fett-Index
I bis II	4·00—3·50
II—III bis III—IV	3·50—2·50
IV bis IV—V	2·50—1·50
V bis VII	1·50—1·00

Für die einzelnen Fanggebiete der Nordsee und die Fangmonate ergaben sich folgende Indices:—

	1953	1954
Nördliche Viking Bank		Ende März 1·10
Südliche Viking Bank		Ende März 1·28 (+1·80)
Bressay Shoal	Juni 2·91	Juni 2·48
		Juli 2·49
		Aug. 2·76
Fladengrund	Juni 3·22	Juni 2·59
	Juli 2·38	Juli 2·49
		Aug. 2·04
Gat	Sept. 1·40	
Long Forties	Juli 3·08	Juli 3·15
Südl. Devil's Hole		Juli 2·73
		Aug. 2·73
N.O.-Bänke		Ende Juli 2·97
Farn Deeps		Sept. 1·88
Östl. Ostbank		Sept. 1·96
Brucey's Garden		Sept. 2·05
		Okt. 1·28
Doggerbank		Okt. 1·04
Mittelriff	Sept. 2·46	Okt. 1·25
Südriff (laichend)		Sept. 1·00
Outer Silver Pit (laichend)		Okt. 1·01
Lemon Bank		Okt. 1·10
Engl. Kanal	Dez. 1·09	Dez. 1·12
Südl. Schlickbank } Ölheringe		Ende Juli 3·30
Weisse Bank } Ölheringe		Ende Juli 3·67
Tail End (Dogger) } Ölheringe		Anf. Sept. 2·22

Aus vorstehender Aufstellung ist im Grossen zu ersehen: Im Frühjahr trifft man in der Gegend der Viking-Bank Herbst- und Winterlaicher verschiedener noch nicht hinreichend geklärter Herkunft in stark wechselndem Mischungsverhältnis. Von Fettansatz ist meist noch nichts zu entdecken, daher die niedrigen Indices etwas über 1·00. Aus April und Mai fehlen bisher Beobachtungen. Im Juni und Juli wird recht starker Fettansatz gefunden, etwa von 2·50 bis über 3·00, wobei nicht wenige Einzeltiere 4·00 erreichen können. Auch im August hält sich der Fettgehalt noch mit guten Werten. Im September wird nur selten die 2·00-Grenze erreicht, auf dem Südriff am Dogger treten die ersten laichenden Heringe auf, das Fett ist dann aus der Leibeshöhle verschwunden (Index 1·00). Im Oktober sind Fettwerte von etwas über 1·00 die Regel, da das Laichen allgemein wird. Die kleinen Ölheringe, die ausnahmslos zur Ölgewinnung in die Industrie wandern, haben im Juli besonders hohe Werte, die sich, da noch keine Laichausbildung stattfindet, bis später ins Jahr verhältnismässig hoch halten.

Summary.

The distribution of the fat tissue (ister) in the ventral cavity of herring caught in different parts of the North Sea and its variations at different stages of sexual maturity have been studied. The quantity of fat present has been recorded numerically, on the following scale:— (1) little fat, (2) fat, (3) very fat, (4) extremely fat.

In spring (March), mixtures of autumn- and winter-spawning herring of different, and as yet uncertain, origin occur in the Viking Bank region. Most of the fish there contain no fat, the index being somewhat over 1. By June and July the amount of fat has increased considerably, to between 2 and 4. In August the index is still high. In September spawning herring make their first appearance on the southern edge of the Dogger Bank. In these fish the fat has disappeared from the ventral cavity (stage 1) and stage 2 is rarely reached. In October, when spawning is proceeding, the average fat value is somewhat over 1.

The small herring, which are all used in the factories for the production of oil, contain most fat in July. As they do not spawn, they remain relatively fat until late in the year.

Some Experiments on Factors Influencing Mesh Selection in Trawls.

By

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Introduction.

The investigations so far made on mesh selection give a general idea of the releasing capacities of meshes of different sizes. Jensen (1949), in his review of the papers on this subject, comes to the conclusion that the length at which the fish has a 50 % chance of escaping through the mesh is directly proportional to the mesh-size (at least up to a mesh-size of 9 cm.). This conclusion is confirmed by Graham, Beverton, Margetts, and Gulland (1954). But Jensen also states that Danish seines tend to have a greater releasing effect than trawls of the same mesh-size.

Margetts (1949) compares the fishing capacities of Danish-seiners and trawlers, and presents data on the differences in selectivity between these two types of gear.

Graham, Beverton, Margetts, and Gulland (1954) made a careful study of the published evidence concerning the differences between seines and trawls. They conclude that the seine liberates relatively larger fish than does the trawl. For plaice this difference is the same as that between trawls differing by 10 mm. in mesh-size. The data on dabs and haddock were too meagre for numerical estimates to be made.

Lucas, Ritchie, Parrish, and Pope (1954) describe the results of new experiments. They show that a Danish seine releases haddock of the same length as a trawl when the mesh-size of the seine is about 10 mm. smaller than that of the trawl. Graham (1954) obtained similar results from his experiments.

It cannot be decided from the existing information whether the differences between the two types of gear are related with the differences

between the twines used for these nets, with other characteristics of the gear, or with the manner of fishing.

M a r g e t t s (1949) presents some facts which support the suggestion that selection by the seine warps might play an important rôle in causing the phenomenon. On the other hand, J e n s e n (1949) is inclined to believe that the stiffness of the twines used for the nets has a considerable effect on mesh selection, for flatfish especially.

The data obtained by L u c a s, R i t c h i e, P a r r i s h, and P o p e (1954) by the covered cod-end method show that a large part at least of the differences between the catches of haddock by seines and trawls is due to mesh selection in the cod-end. Differences between the types of twine used for the nets, between towing speeds, etc., exist not only for trawls and Danish seines, but also amongst trawls of different types, as used, for instance, by trawlers of various sizes.

It is becoming more and more desirable to reach an understanding of the way in which these differences influence mesh selection, and their extent. This is the more important since international mesh regulations have come into force. In our investigations we have studied the releasing capacity of cod-ends made of two different types of twine. Some preliminary experiments have been done on the effect of towing speed on mesh selection.

Mesh Selection in Cod-Ends made of Different Twines.

Methods.

In these experiments the selectivities of cod-ends made of hemp, running 510 metres per kilogramme, and of manila, running 250 metres per kilogramme, have been studied by the covered cod-end method. Both hemp and manila twines were 3-ply. The diameter of the hemp twine was about two-thirds, and its flexibility about $2^1/_2$ times, that of the manila twine. The 510 m./Kg. hemp is normally used in the Dutch inshore fishing vessels, whereas the 250 m./Kg. manila is often used for the trawls of the larger vessels.

All cod-ends were double braided, and tanned. They were covered with netting of 3-cm. mesh. The cover was attached in such a manner that the whole of the cod-end, the "back" as well as the "belly" part, was enclosed in an outer cover. The cover was kept clear of the cod-end by cane hoops. The "false bellies" were attached outside the cover. The hauls were of 3 hours duration. The average towing speed was 2·6 miles per hour. The experiments were carried out in the area between 52°20′N. and 53°20′N., and between 3°30′E. and the Dutch coast, in the period from January until July 1954.

The species of fish studied in these investigations were plaice, sole, dab, and whiting. The quantities of plaice, sole, and whiting of the length frequencies relevant to our investigations were rather small. We therefore paid much attention to the dabs, which were always present in large numbers.

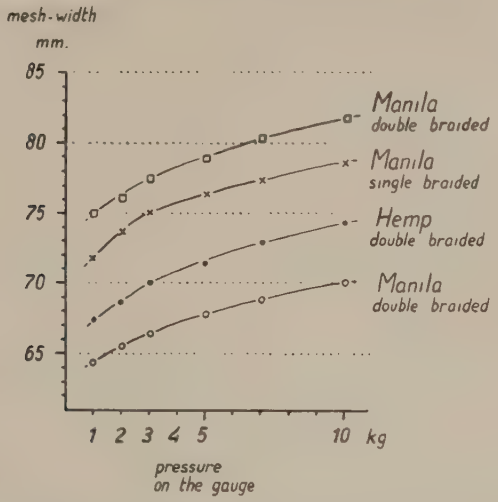

Figure 1. Relationship between the force with which the gauge is pushed into the mesh and the observed mesh-size, for four different cod-ends (measured wet). Each point represents the average of 30 measurements. (Data from J. F. de Veen).

Determination of mesh-size.

It is obvious that the mesh-size concerned in mesh selection is that of the lumen of the mesh, when the net is wet and in use. This size is generally measured by means of a flat gauge, narrower at one end than at the other, and inserted into the mesh until it can go no further. The figure obtained in this way is influenced by the force with which the gauge is pushed into the mesh (Figure 1). It has often been stressed that "no force" should be used. This can be achieved approximately if the mesh is first stretched and the gauge inserted in that position. But this is not often practicable. Usually the mesh is stretched by pushing the gauge into it — an action which needs some force. It appeared in our investigations that this force may very readily amount to more than 2 Kg., whereas the observer at that moment hardly realizes he is using any force at all.

The usual practice is to push the gauge into the mesh until a distinct resistance is felt. What is judged to be a distinct resistance depends to a certain degree on the observer. We found that in our mesh-size estimations the force put on the gauge was about 4 Kg. In the course of our investigations a gauge with a pressure indicator has been developed. The angle between the sides of the gauge is 30°, and the measuring part is 2 mm. thick, with slightly rounded edges. With this gauge we always measured with a pressure of 4 Kg., when the net was wet, before and after each haul.

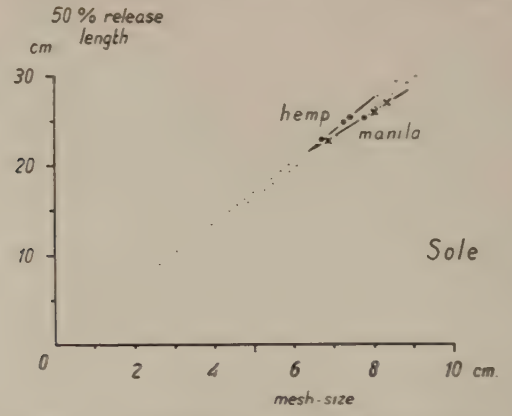

Figure 2. Relationship between observed 50 % points for sole and mesh-size for manila and hemp cod-ends.

Results.

A number of hauls have been made with hemp and manila cod-ends of mesh-sizes between 67 and 83 mm. The totals of all hauls for each fish species and cod-end are given in Tables 1—4, together with the average mesh-size of the cod-end in the relevant hauls. From these data selection ogives have been constructed, and 50 % points estimated. The 50 % points are plotted in Figures 2—5. Straight lines have been drawn through the points relating to the hemp and to the manila cod-ends (in drawing these lines and in the figures given below, the data for the hemp cod-end of 77 mm. mesh, though plotted in the graphs, have been disregarded, for reasons explained later).

If the lines obtained in this way are extrapolated, none of them

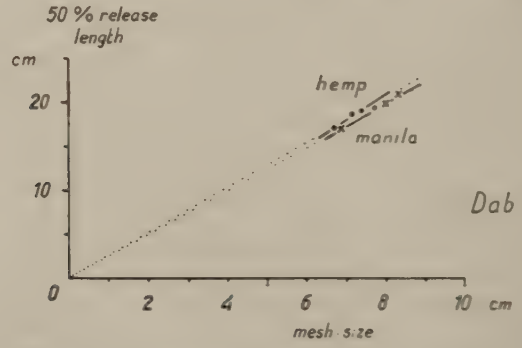

Figure 3. Relationship between observed 50 % points for dab and mesh-size for manila and hemp cod-ends.

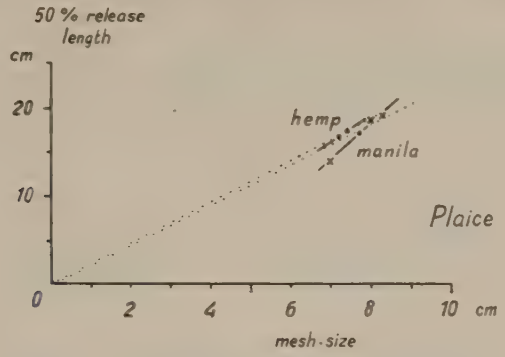

Figure 4. Relationship between observed 50 % points for plaice and mesh-size for manila and hemp cod-ends.

passes through the origin, but there appears to be no systematic deviation from direct proportionality between mesh-size and 50 % point. But the lines for the dab pass very close to the origin, and the results for the dab are considered to be the most reliable, because they are based on the largest numbers of hauls and of fish. It thus appears that the deviations may be ascribed to sampling variation. We have therefore no reason to suppose that our data contradict the published evidence about the direct proportionality between the length of the fish at the 50 % point and the mesh-size.

The direct proportionality being accepted, we proceeded to calculate the average values of the ratio 50 % point/mesh-size for each cod-end

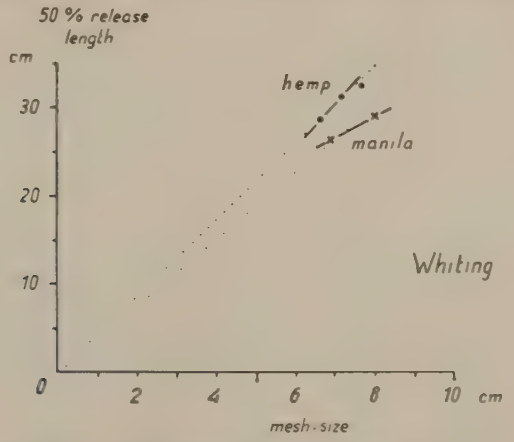

Figure 5. Relationship between observed 50 % points for whiting and mesh-size for manila and hemp cod-ends.

Table 1.

Length frequency distributions of Sole caught in the cod-end and in the cover, with hemp and manila cod-ends of different mesh-sizes.

HEMP

Number of hauls	11			21			16			9		
Mesh-size	67 mm.			72 mm.			74 mm.			77 mm.		
	Numbers in:		% in cod-end	Numbers in:		% in cod-end	Numbers in:		% in cod-end	Numbers in:		% in cod-end
cm.	cod-end	cover		cod-end	cover		cod-end	cover		cod-end	cover	
19—20	—	11	0	—	—	—	1	20	5	—	5	0
20—21	3	14	18	—	—	—	2	28	7	3	4	43
21—22	3	11	22	—	11	0	3	28	10	3	6	33
22—23	15	18	45	2	32	6	6	45	12	5	10	33
23—24	33	23	59	16	36	31	14	80	15	4	14	22
24—25	69	7	91	23	47	33	40	89	31	13	12	52
25—26	78	3	96	59	17	78	82	64	56	26	21	55
26—27	108	5	96	60	13	82	97	52	65	27	9	75
27—28	120	6	95	74	6	93	154	19	89	46	5	90
28—29	101	2	98	79	2	98	132	5	96	62	3	95
29—30	113	6	95	72	—	100	113	2	98	38	1	97
30—31	68	1	99	49	1	98	85	—	100	29	—	100
31—32	62	—	100	42	—	100	67	—	100	28	—	100
32—33	55	—	100	37	—	100	38	—	100	19	—	100
50 % point:	22·9 cm.			24·8 cm.			25·4 cm.			25·2 cm.		

MANILA

Number of hauls	19			6			5		
Mesh-size	68 mm.			80 mm.			83 mm.		
	Numbers in:		% in cod-end	Numbers in:		% in cod-end	Numbers in:		% in cod-end
cm.	cod-end	cover		cod-end	cover		cod-end	cover	
19—20	—	21	0	1	5	17	—	2	0
20—21	5	32	13	—	7	0	—	5	0
21—22	5	21	19	1	7	13	—	7	0
22—23	12	17	41	3	22	12	2	9	18
23—24	27	10	73	4	20	17	2	17	11
24—25	38	21	64	5	11	31	7	24	23
25—26	48	6	89	14	14	50	9	30	23
26—27	36	—	100	10	11	48	20	25	44
27—28	55	2	96	21	5	81	39	27	59
28—29	61	2	97	27	—	100	61	6	91
29—30	48	1	98	15	—	100	47	4	92
30—31	36	—	100	25	—	100	41	1	98
31—32	39	—	100	13	—	100	33	1	97
32—33	32	—	100	—	—	—	20	—	100
50 % point:	22·8 cm.			26·0 cm.			27·1 cm.		

Note: The numbers of fish of the length frequencies irrelevant to our investigations have been omitted from this and the following tables. The small fish not included in the tables were almost all in the cover, and all the larger ones were in the cod-end.

Table 2.

Length frequency distributions of Dab caught in the cod-end and in the cover, with hemp and manila cod-ends of different mesh-sizes.

HEMP

amber hauls fesh-size	10			29			11			5		
	67 mm.			71 mm.			74 mm.			77 mm.		
cm.	Numbers in: cod-end	cover	% in cod-end	Numbers in: cod-end	cover	% in cod-end	Numbers in: cod-end	cover	% in cod-end	Numbers in: cod-end	cover	% in cod-end
—11	1	215	0	3	546	1	—	49	0	1	73	1
—12	3	302	1	6	747	1	1	64	1	1	99	1
—13	2	378	1	12	1026	1	2	151	1	1	191	1
—14	9	491	2	17	1522	1	6	296	2	5	325	2
—15	31	639	5	31	1968	2	7	566	1	12	690	2
—16	102	639	14	59	2737	2	17	612	3	31	906	3
—17	307	640	32	193	3343	5	52	1165	4	78	1225	6
—18	740	335	69	746	2958	20	162	1256	11	178	1413	11
—19	931	87	91	1485	1643	47	347	635	35	417	924	31
—20	735	10	99	1468	351	81	415	165	72	506	293	63
—21	393	1	100	832	32	96	302	20	94	362	43	89
—22	199	—	100	492	4	99	142	2	99	197	2	99
—23	115	—	100	303	4	99	110	—	100	93	1	99
—24	—	—	—	176	—	100	53	—	100	61	—	100
—25	—	—	—	—	—	—	19	—	100	31	—	100
% point:	17·0 cm.			18·6 cm.			18·9 cm.			19·1 cm.		

MANILA

mber hauls esh-ize	22			10			5		
	68 mm.			80 mm.			83 mm.		
m.	Numbers in: cod-end	cover	% in cod-end	Numbers in: cod-end	cover	% in cod-end	Numbers in: cod-end	cover	% in cod-end
—11	3	503	1	—	—	—	—	—	—
—12	6	672	1	—	135	0	—	53	0
—13	38	1415	3	—	300	0	—	91	0
—14	87	2378	4	10	677	1	—	154	0
—15	240	3276	7	30	1270	2	4	290	1
—16	673	3518	16	74	1761	4	8	409	2
—17	1595	2723	37	193	2239	8	14	562	2
—18	2862	1218	70	326	2031	14	26	710	4
—19	2514	221	92	431	1328	25	37	675	5
—20	1668	36	98	459	570	45	85	475	15
—21	787	11	99	418	158	73	112	186	38
—22	436	2	100	309	18	94	115	33	78
—23	271	—	100	182	—	100	90	6	85
—24	—	—	—	95	—	100	56	—	100
—25	—	—	—	—	—	—	18	—	100
% point:	16·9 cm.			19·7 cm.			20·8 cm.		

Table 3.

Length frequency distributions of Plaice caught in the cod-end and in the cover, with hemp and manila cod-ends of different mesh-sizes.

HEMP[1])

Number of hauls	21			5			7		
Mesh-size	72 mm.			74 mm.			77 mm.		
cm.	Numbers in: cod-end	cover	% in cod-end	Numbers in: cod-end	cover	% in cod-end	Numbers in: cod-end	cover	% in cod-end
10—11	—	—	—	—	—	—	—	—	—
11—12	—	2	0	—	2	0	—	71	0
12—13	1	2	33	—	5	0	2	82	2
13—14	—	8	0	—	16	0	—	76	0
14—15	—	13	0	—	29	0	4	83	5
15—16	7	86	8	2	24	8	2	67	3
16—17	154	264	37	24	77	24	43	112	28
17—18	794	149	84	142	108	57	219	123	64
18—19	1103	33	97	410	51	89	558	68	89
19—20	977	4	100	592	7	99	775	16	98
20—21	789	1	100	552	2	100	737	5	99
21—22	676	—	100	518	—	100	583	1	100
22—23	—	—	—	449	—	100	489	—	100
23—24	—	—	—	—	—	—	437	—	100
50 % point:	16·8 cm.			17·3 cm.			17·1 cm.		

MANILA

Number of hauls	4			14			5		
Mesh-size	70 mm.			80 mm.			83 mm.		
cm.	Numbers in: cod-end	cover	% in cod-end	Numbers in: cod-end	cover	% in cod-end	Numbers in: cod-end	cover	% in cod-end
10—11	—	1	0	—	—	—	—	—	—
11—12	7	12	37	—	1	0	—	2	0
12—13	4	11	27	—	1	0	—	4	0
13—14	3	13	19	1	28	3	—	6	0
14—15	39	21	65	1	64	2	—	13	0
15—16	90	23	80	2	125	2	1	10	9
16—17	354	34	91	26	321	7	3	59	5
17—18	877	7	99	124	615	17	12	198	6
18—19	1044	2	100	433	493	47	159	330	33
19—20	873	—	100	606	104	85	471	203	70
20—21	—	—	—	536	9	98	654	30	96
21—22	—	—	—	416	2	100	563	2	100
22—23	—	—	—	432	—	100	500	—	100
23—24	—	—	—	322	—	100	—	—	—
50 % point:	13·9 cm.			18·6 cm.			19·0 cm.		

[1]) For the 67 mm. mesh-size we have no data.

and each species of fish. The 50 % points used for this purpose were those estimated from the selection ogives obtained for the separate cruises, not from the totals of all cruises for each cod-end given in Table 1. In determining a single ratio for each species the relative numbers of fish caught on the separate cruises have been taken into account.

The values found are:—

	Sole	Dab	Plaice	Whiting
Manila cod-end	3·31	2·46	2·28	3·80
Hemp cod-end	3·44	2·56	2·33	4·33

The 50 % points for a mesh-size of 75 mm.[1]), calculated from these values, are:—

	Sole	Dab	Plaice	Whiting
Manila cod-end	24·8	18·5	17·1	28·5
Hemp cod-end	25·8	19·2	17·5	32·5

It appears from these figures that in every case the hemp cod-end releases larger fish than does the manila. The mesh-size at which the hemp cod-end releases the same length of fish as a manila cod-end of 75 mm. mesh can be calculated from the formula ratio manila/ratio hemp × 75 mm. For soles this figure is 72 mm., for dabs 72 mm., for plaice 73 mm., and for whiting 66 mm. The data for plaice may be regarded as the least reliable of our figures. The conclusion seems justified that the difference in mesh selection for all flatfish amounts to 3 mm. in the mesh. For whiting the difference is much greater, about 9 mm.

In another paper in which the same data are employed (B o e r e m a, 1954), for the sake of simplicity the figures have not been calculated from the ratio 50 % point/mesh-size, but estimated from the curves in the diagram. The results are practically identical with those stated here, showing a difference of 3 mm. in the mesh for soles and dabs, of 4 mm. for plaice, and of 10 mm. for whiting. The estimated 50 % points at a mesh-size of 75 mm. differ slightly from those given in this paper.

In these considerations the data for the hemp cod-end of 77 mm. mesh have not been taken into account. The reason is that this cod-end, a new one, was used on one cruise only, and on that cruise the gauge fitted with the pressure indicator was not available. On the next cruise the same cod-end was found to have a 74 mm. mesh. Shrinkage may have occurred, but it seems more probable that on the first cruise, when the cod-end mesh was recorded as 77 mm., the force used in pressing the gauge into the mesh was greater than normal, so that the mesh-size was read wrongly. If the mesh on this cruise was in fact 74 mm., the results accord much better with the data for the other cod-ends.

[1]) Figures have been calculated for a mesh-size of 75 mm. because that is the minimum mesh-size adopted for the North Sea, since 1954.

Table 4.

Length frequency distributions of Whiting caught in the cod-end and in the cove with hemp and manila cod-ends of different mesh-sizes.

HEMP

Number of hauls	11			15			10			7		
Mesh-size	67 mm.			72 mm.			74 mm.			77 mm.		
cm.	Numbers in: cod-end	cover	% in cod-end	Numbers in: cod-end	cover	% in cod-end	Numbers in: cod-end	cover	% in cod-end	Numbers in: cod-end	cover	% in cod-end
19—20	—	42	0	—	46	0	—	13	0	—	38	0
20—21	1	63	2	2	68	3	—	22	0	—	69	0
21—22	4	121	3	2	134	2	2	25	7	—	123	0
22—23	8	188	4	4	168	2	—	51	0	—	140	0
23—24	12	208	5	5	300	2	1	83	1	3	218	1
24—25	17	168	9	10	322	3	1	82	1	3	184	2
25—26	27	131	17	18	297	10	1	80	1	10	151	6
26—27	54	113	32	30	296	9	3	84	3	8	136	6
27—28	43	67	39	46	217	17	3	59	5	5	69	7
28—29	36	33	52	44	141	24	1	56	2	15	65	19
29—30	26	18	59	40	95	30	8	48	14	9	39	19
30—31	24	11	69	34	48	41	5	12	29	7	16	30
31—32	23	3	88	38	28	58	4	9	31	7	12	37
32—33	21	1	95	24	19	56	2	6	25	7	4	64
33—34	12	—	100	19	2	90	1	7	13	5	4	56
34—35	5	—	100	11	4	73	1	6	14	6	—	100
35—36	7	—	100	11	2	85	3	2	60	4	1	80
36—37	—	—	—	4	—	100	2	2	50	—	1	0
37—38	—	—	—	5	—	100	1	1	50	—	—	—
50 % point:	28·5 cm.			31·3 cm.			?			32·4 cm.		

The Relation between Towing Speed and Mesh Selection.

It is often suggested that towing speed might influence mesh selection, and we have examined the data from the experiments described above to obtain information on this subject. In these experiments fishing was carried out at constant engine revolutions. This resulted in the towing distance varying with the tide. When the haul is made with the tidal current, the current raises the ship's speed over the ground above that given by the propeller through the water. But close to the bottom this current is much weaker than near the surface, and accordingly the speed of the trawl through the water increases when the speed of the ship is increased by the current. In order to study the effect of this on mesh selection, we plotted the 50 % points for each haul against towing distance, estimated with the aid of the Decca Navigator. This could be done only for dabs, as the 50 % points on each haul could not be determined for other fish. Figures 6 and 7 show that the 50 % points are not appreciably influenced by the variation in distance covered.

Table 4 (continued).

MANILA

Number of hauls	24			5			3		
Mesh-size	69 mm.			80 mm.			83 mm.		
cm.	Numbers in: cod-end	cover	% in cod-end	Numbers in: cod-end	cover	% in cod-end	Numbers in: cod-end	cover	% in cod-end
19—20	3	172	2	—	29	0	—	13	0
20—21	12	246	5	2	50	4	—	31	0
21—22	38	421	8	2	103	2	—	52	0
22—23	61	683	8	4	196	2	2	85	2
23—24	117	664	15	6	238	2	—	102	0
24—25	207	554	27	22	256	8	4	97	4
25—26	246	397	38	21	238	8	4	65	6
26—27	288	251	53	48	161	23	1	65	2
27—28	265	149	64	71	125	36	2	28	7
28—29	230	64	78	56	79	41	5	24	17
29—30	175	32	85	56	43	57	6	15	29
30—31	150	14	91	45	25	64	4	3	57
31—32	115	—	100	36	16	69	3	3	50
32—33	62	1	98	25	5	83	2	2	50
33—34	51	1	98	19	3	86	—	1	0
34—35	33	—	100	20	4	83	2	—	100
35—36	27	—	100	13	1	96	—	1	0
36—37	24	—	100	9	—	100	3	—	100
37—38	—	—	—	6	—	100	2	—	100
50 % point:	26·3 cm.			29·1 cm.			?		

More direct data have been obtained from a few alternate hauls made at different towing speeds (400 and 500 revs., giving average speeds of 2·3 and 3·1 miles per hour). Only data for dabs were obtained; these are given in Table 5. For the hemp 66-mm. cod-end the 50 % point is 17·2 cm. at 400 revs., and 17·7 at 500 revs. For the hemp 72-mm. cod-end the figures are 18·7 cm. at 400 revs., and 18·1 at 500 revs. In the first experiment the 50 % point was somewhat higher at the higher speed than at the lower, whereas in the second experiment, the reverse was the case. It may therefore be concluded from our experiments that the effect of towing speed on mesh selection is not appreciable.

Control Experiments with Covered Cod-Ends.

It is possible that our results are affected by the covered cod-end method. D a v i s (1934) came to the conclusion that the cover had a masking effect on the possibility of the fish escaping. But in D a v i s's experiments the cover was attached round the upper side of the cod-end only. The "belly" was lined with small-mesh netting, to prevent fish

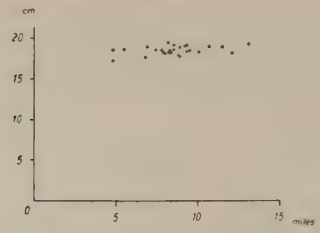

Figure 6. Relationship between towing distance (3-hour haul) and 50 % point of dab. Hemp cod-end, mesh-size 71 mm.

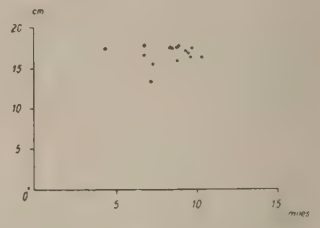

Figure 7. Relationship between towing distance (3-hour haul) and 50 % point of dab. Manila cod-end, mesh-size 68 mm.

escaping through this part of the trawl, as certainly happens with normal cod-ends. It is possible that the fish's chance of escape is diminished by lining the under side of the cod-end. If that is the case, 50 % points calculated from D a v i s' s experiments are too low.

Notwithstanding his remarks that covered-net experiments are unreliable, D a v i s states that in a special experiment, devised to show the relative efficiency of covered and uncovered cod-ends, the masking effect of the cover was comparatively slight. In order to avoid the possibility of error caused by lining the under side, we used a cover which enveloped the whole cod-end. However, if this cover has in fact had a masking effect, our main conclusions regarding the difference in mesh selection exhibited by cod-ends of different twines are not invalidated, since the masking effect may be taken as having affected the results of all cod-ends in the same way.

To discover whether this effect has occurred in our investigations, some preliminary experiments have been undertaken. If the masking effect of the cover arises from its influence on the flow of water through the cod-end, this influence may be largely removed by leaving the cover open. We therefore carried out alternate hauls with the cover open and closed. All hauls were made in the same locality. The length distributions of the fish caught in the cod-end are shown in Figures 8 and 9; these indicate no important difference between the catches with open and closed covers. Cod-ends with and without covers were also used in a few other hauls (Figures 10 and 11), and these too show no effects from the cover. In these experiments, many small fish were present on the grounds, and they were taken in large quantities in the cover, when it was closed.

In investigations on the influence of towing speed, more serious objections may be made against the covered cod-end method. It is suggested that the towing speed might have an influence on mesh selection because of the fact that at higher speeds the water pressure on the meshes is greater than at slow. It is possible that the cover, because of its small mesh, "overflows" at higher speeds, but in that case the water pressure on the mesh of the cod-end may remain the same. Then

Table 5.

Length frequency distributions of Dab caught in the cod-end and the cover for different towing speeds, with hemp 66 and 72 mm. cod-ends.

	66 mm.						72 mm.					
Number of hauls / Revolutions	4 / 400			5 / 500			4 / 400			3 / 500		
	Numbers in:		% in cod-end	Numbers in:		% in cod-end	Numbers in:		% in cod-end	Numbers in:		% in cod-end
cm.	cod-end	cover		cod-end	cover		cod-end	cover		cod-end	cover	
10—11	—	18	0	—	24	0	—	—	—	—	—	—
11—12	1	21	5	—	16	0	—	—	—	—	33	0
12—13	—	46	0	—	47	0	—	9	0	1	18	5
13—14	3	111	3	—	91	0	—	66	0	—	34	0
14—15	5	243	2	2	236	1	1	124	1	—	42	0
15—16	23	300	7	11	322	3	1	206	1	6	59	9
16—17	93	260	26	53	351	13	8	399	2	10	122	8
17—18	224	155	59	185	250	43	62	622	10	53	135	28
18—19	235	31	88	258	68	79	268	416	39	100	62	62
19—20	133	2	99	171	5	97	378	83	82	124	19	87
20—21	66	—	100	109	—	100	207	9	96	68	2	99
21—22	36	—	100	55	—	100	126	2	98	40	2	95
22—23	24	—	100	12	—	100	85	2	98	14	1	93
23—24	6	—	100	14	—	100	42	—	100	14	—	100
24—25	5	—	100	5	—	100	18	—	100	4	—	100
50 % point:	17·2 cm.			17·7 cm.			18·7 cm.			18·1 cm.		

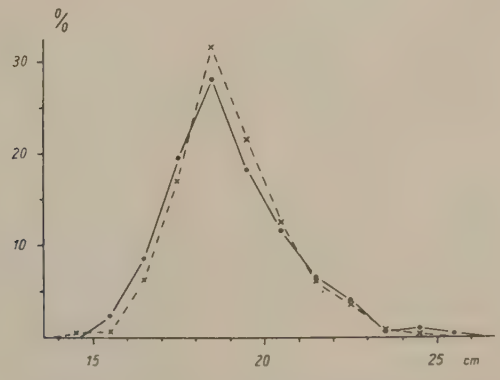

Figure 8. Length frequency distributions of dab caught in a covered 72 mm. hemp cod-end, cover closed and open.
· · · cover closed, 6 hauls, 546 fish.
x - - - x cover open, 5 hauls, 520 fish.

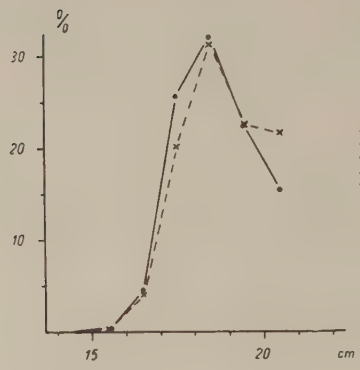

Figure 9. Length frequency distributions of plaice caught in a covered 72 mm. hemp cod-end, cover closed and open.
•——• cover closed, 6 hauls, 1287 fish.
x - - - x cover open, 5 hauls, 855 fish.

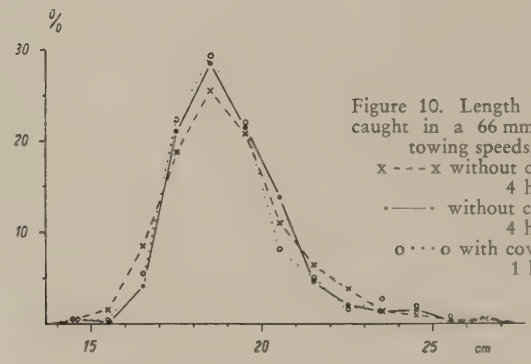

Figure 10. Length frequency distributions of dab caught in a 66 mm. hemp cod-end, at different towing speeds, with and without cover.
x - - - x without cover, 400 engine revolutions, 4 hauls, 639 fish.
•——• without cover, 490 engine revolutions, 4 hauls, 511 fish.
o · · · o with cover, 400 engine revolutions, 1 haul, 260 fish.

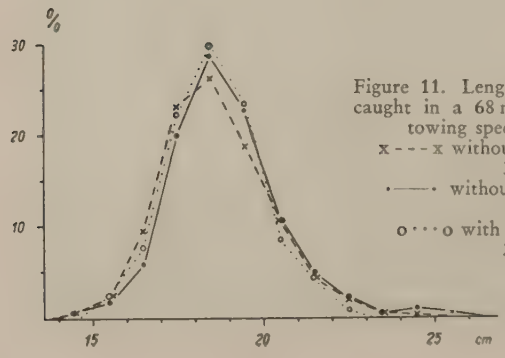

Figure 11. Length frequency distributions of dab caught in a 68 mm. manila cod-end, at different towing speeds, with and without cover.
x - - - x without cover, 400 engine revolutions, 3 hauls, 3015 fish.
•——• without cover, 490 engine revolutions, 2 hauls, 935 fish.
o · · · o with cover, 400 engine revolutions, 2 hauls, 1249 fish.

the effect of towing speed on mesh selection would not be shown by our experiments.

In order to check our results a few experiments have been carried out with alternate hauls at different towing speeds (400 and 490 revs.) with an uncovered cod-end. The length distributions of the catches are shown in Figures 10 and 11. In this case again, the graphs are almost identical.

The experiments described are not numerous, and the results they furnish cannot be taken as definite. But at any rate they do not suggest that the results described above are adversely affected by the covered cod-end method.

Discussion.

Investigations have shown that mesh selection is affected by the type of twine from which the trawl is made. A cod-end made of thin and relatively flexible twine releases larger fish than one of stiffer material, for the same size of mesh. The magnitude of this effect is not the same for each species of fish. The difference between the 50 % points obtained with the twines used in our experiments is fairly small, being about the same for dab, sole, and plaice, but much larger for whiting. It is suggested that these results are connected with characteristic differences between flatfish and roundfish. They are contrary to Jensen's supposition that flatfish would be affected to a greater extent than roundfish. The explanation of this phenomenon may be found in the action of the cod-end during towing, and especially in the shape of the meshes and the forces acting on them.

The question arises whether our results reflect a peculiarity of the trawl used in our experiments, an ordinary Dutch trawl, or are applicable to all types of towed gear. The only evidence on this subject is to be found in the papers on mesh selection in the Danish seine. Bowman (1928) considered the difference in mesh selection between trawls and Danish seines to be smaller for flatfish than for haddock. Certain remarks in the paper by Lucas, Ritchie, Parrish, and Pope (1954) seem to confirm this.

Graham, Beverton, Margetts, and Gulland (1954) estimated that the difference in mesh selection between seines and trawls amounted to 10 mm. in the mesh in the case of plaice. Lucas, Ritchie, Parrish, and Pope, and also Graham (1954), found the same figure for haddock. But the figure for plaice is estimated with the proviso "that it is impracticable to be very precise in this matter", and seems liable to some doubt. The scanty evidence available seems to suggest that the phenomenon found in our investigations is not confined to our type of trawl.

The figures obtained from our experiments are rather different from those given by Jensen. For the ratio 50 % point/mesh-size he found values of 2·0 for plaice, of 2·2 for dab, of 3·1 for whiting, and of 3·5 for sole. In order that our trawl with a manila cod-end should select

fish of the same size as would a trawl with 75 mm. mesh and giving the above ratios, our trawl would — according to our experiments — require a mesh-size of 66 mm. for plaice, 67 mm. for dab, 61 mm. for whiting, and 79 mm. for soles.

Graham, Beverton, Margetts, and Gulland mention a value for the ratio 50 % point/mesh-size of 2·18 for plaice. With our trawl this would give a difference of 3 mm. in the mesh. In the English paper it is stated that the mesh measurements are assumed to have been made without forcing the gauge into the mesh. If in fact no force was used, then the force of 4 Kg. used in our investigations is equivalent to a mesh-size difference of 4 mm. (Figure 1). According to this calculation the difference between the selective action of the English trawl and our trawl with a manila cod-end amounts to 7 mm. in the mesh in the case of plaice.

These calculations indicate fairly large differences between the mesh selection in our trawl and that in the trawls used in other investigations. The reality of these differences does not seem to be very certain, however, and needs further confirmation. One of the possible factors causing the differences between the values of the ratio 50 % point/mesh-size in the various papers lies in the method of measuring the mesh-size. It is apparent that standardization of the methods of mesh-size determination is required, if comparable results from different investigations are desired.

Another possible factor causing the differences between the results of the various investigations might be variations in towing speed. Our few experiments on this subject provide no definite evidence, but they suggest that variations in towing speed, so long as they are not extreme, have little effect. They need further confirmation, however.

It is suggested that the covered cod-end method has not affected our results.

Further investigations on the factors influencing mesh selection might serve to furnish a much better understanding of the principles underlying mesh selection.

Summary.

The difference in mesh selection between hemp and manila cod-ends has been studied by the covered cod-end method.

The hemp cod-end releases larger fish than does the manila.

A manila cod-end of 75 mm. releases flatfish at the same length as a hemp cod-end of 72 mm., and whiting at the same length as a hemp cod-end of 66 mm. (hemp running 510 m./Kg., manila 250 m./Kg.).

The influence of towing speed on mesh selection could not be shown.

Our results have not been influenced by the covered cod-end method.

Standardization of the methods of determination of mesh-size seems advisable.

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Reviews.

J. Chase. "A comparison of certain North Atlantic wind, tide gauge and current data". Journ. Mar. Res., **13**, 1, pp. 22—31, 5 figs. New Haven, Conn., 1954.

The studies made by numerous oceanographers, notably M u n k, seem to have established the fact that the major features of the great oceanic current systems correspond fairly well with the average wind conditions. It is also a fact, however, that the transports of the currents vary with time over a fairly wide range. The factors determining these variations are still little known. A theoretical study by S t o m m e l (Techn. Rep., Nos. 51—57, Woods Hole Oceanogr. Inst., 1951) indicates that the density distribution in the ocean is not likely to respond to wind variations of periods of less than several years, but it is doubtful whether his very much simplified analysis is applicable to the actual ocean.

The present study may be considered as an empirical approach to the problem. The author makes a comparison between observed tide-gauge heights, winds, and currents. The best agreement is found between the geostrophic winds and the surface currents in the region of the trade winds and also south of C. Hatteras. A maximum occurs in summer in all these curves, without any appreciable time-lag.

The variation in sea-level height does not correspond so well with the variation in the strength of the trade winds. The author therefore adds the trades and the westerlies (geostrophic) together, and so obtains a better agreement with the sea-level data, but the significance of this addition is not obvious to the reviewer. In any case, the summer maximum in the wind curves is distinctly reflected in the sea-level curves, and this may indicate that the density distribution responds to wind variations of periods of one year or less.

The author has also studied the variation of short-period averages (three-month running means) of trades plus westerlies and of sea-level (Miami, Galveston, difference Bermuda—Charleston) over a term of three years. There is no clear-cut correspondence, but some of the more prominent features are common to all the curves.

O. H. Sælen.

I. Hela. "The surface current field in the western part of the North Atlantic". Bull. Mar. Sci. Gulf and Carribean, **3**, 4, pp. 241—72, 22 figs. Miami, 1954.

Using the U. S. Hydrographic Office charts of the monthly mean current vectors for one-degree squares of latitude and longitude, the author has

computed mean values of the current for each of the four seasons and for the whole year. The values thus obtained have been used to compute the horizontal divergence $\frac{\partial v_x}{\partial x} + \frac{\partial v_y}{\partial y}$ at each intersection of 1° lines of latitude and longitude in the area under consideration, for the different seasons and for the year as a whole. The results are presented in charts. The most prominent features of the divergence distribution are the area of convergence on the left of the Gulf Stream axis and the area of divergence on the right of it, approximately between latitudes 33° and 38°N. The author attempts to bring this feature into relation with the vorticity equation by assuming a certain amount of cross-stream variation in the friction.

A very pronounced region of convergence is also found in the region in which the Antilles Current joins the Gulf Stream.

By means of the equation of continuity $\frac{\partial v_x}{\partial x} + \frac{\partial v_y}{\partial y} + \frac{\partial v_z}{\partial z} = 0$ the vertical velocity can be estimated (sea surface assumed to be stationary and surface horizontal divergence assumed to be representative of a given vertical column), and the author arrives at a value of a reasonable order of magnitude, 10^{-3}, at the depth of 70 metres.

O. H. Sælen.

M. J. Pollak. "Static stability parameters in oceanography." Journ. Mar. Res., **13**, 1, pp. 101—12, 2 figs. New Haven, Conn., 1954.

Some forty years ago, Hesselberg and Sverdrup derived a formula for the degree of vertical stability of motionless sea water, which depends essentially on the difference between the observed vertical mass distribution and the mass distribution corresponding to neutral (adiabatic) equilibrium. In the paper under review, the author derives substantially the same formula under several modified forms. That part of the formula which involves the adiabatic gradient may be expressed in terms of the speed of sound in sea water, and the author shows that the application of the formula may be facilitated by graphs based on a knowledge of this speed for different temperatures, salinities, and pressures.

Up to the present time, this precise method of calculating the degree of static stability does not appear to have been much used.

J. P.

O. J. Østvedt. "Zooplankton investigations from Weather Ship M in the Norwegian Sea, 1948—49". Hvalrådets Skr., 40, pp. 1—93, 25 figs. Oslo, 1955.

Mr. Østvedt deals with one facet of the many-sided programme of scientific work which is undertaken by the Norwegian Ocean Weather Ships in addition to their meteorological observations. He reports on the zooplankton which was collected at Station M (66°N., 2°E.) with a Nansen closing net from October 1948 to November 1949. It is most creditable that his objective to take five vertical hauls each week — from 50 m. to the surface, 100 to 50 m., 600 to 100 m., 1,000 to 600 m., and 2,000 (or bottom) to 1,000 m. — was so nearly achieved; 201 hauls were completed despite the difficult conditions which must have often prevailed during the winter.

After discussing the contemporary hydrography, he considers his results under three main headings: the fluctuations in the composition of the plankton

in surface, intermediate, and deep water-layers; the gross seasonal changes in the vertical distribution of the more important copepods; and a series of observations on the life histories, the times of occurrence, and the abundance of a comprehensive list of species. Such an orderly arrangement inevitably leads to some repetition — changes in vertical distribution are relevant to all three topics — but it does facilitate reference, and one expects this paper will be frequently consulted by planktologists.

Throughout the survey, copepods predominated at all depths; the autochthonous species *Calanus finmarchicus* and *Pseudocalanus minutus* being particularly important numerically. There were, however, differences between the plankton communities at various depths, many of which could be attributed to the marked seasonal changes in the vertical distribution of the commoner species. All hauls were made in daylight and so are strictly comparable. But, in consequence, there is no evidence of how diurnal vertical migration may have influenced the picture or have contributed to spreading the plankton over the different water-layers. The 600—100 m. hauls were designed to sample the core of the Atlantic drift and 19 species of more southerly origin were restricted to such depths. However, these were caught in only small numbers while other more abundant forms which may be accepted also as "indicators" of Atlantic influence were found both above and below.

Østvedt, quite rightly, stresses the importance of seasonal vertical migration in the life history of the three species he discusses in most detail. *Calanus hyperboreus*, *C. finmarchicus*, and *Pseudocalanus minutus* all moved towards the surface layers to spawn in early spring and returned to deeper water in mid-summer, but there were distinct differences in the behaviour of the three. Whereas the wintering stock of *C. hyperboreus* comprised a mixture of copepodid stages III to VI, those of both *C. finmarchicus* and *P. minutus* were almost entirely of stage V. While *C. finmarchicus* moulted to maturity during and after the upward migration, *P. minutus* did so before or during the ascent. In the cases of *C. hyperboreus* and *P. minutus* there was a single spring spawning after which the entire population returned to the depths, but, whereas this was also true for the majority of *C. finmarchicus*, a small proportion of this species moulted through to the adult stage near the surface and gave rise to a second summer generation. During most of the year, therefore, the population consists of two different age-groups, one approximately six months older than the other, a fact which might help to explain some of the size-frequency distributions found by other workers. When two size-groups of *Calanus* have been found near together, they have usually been attributed to different geographical origins of two distinct stocks.

The paper includes also some interesting conjecture about the type of stimuli which may evoke the spring migration from the depths. As Østvedt comment, animals living below 1,000 m. can hardly be under the direct influence of light, and other parameters, such as temperature, which have often been associated with vertical movements remain constant throughout the year at such depths. He also disposes of the possibility of "internal waves" carrying the entire population upwards and finally concludes that some cumulative metabolic effect — the approach of maturity, for example — is the most likely factor. On the evidence contained in the paper, however, this does leave the reader with a new problem — the question of how the two broods of *C. finmarchicus*, the spring one a full year old and the autumn one about six months old, both attain the necessary threshold value at the same time, although they have lived under identical environmental conditions.

The simultaneous migration of several different copepodid stages also presents minor difficulties in such an explanation.

While reading Østvedt's account, one cannot fail to appreciate the enormous potentiality of the Weather Ships for augmenting conventional research ship cruises; one is reminded again of the advantages of regular observations from a single station, or a restricted area, to provide extra detail. The Committee responsible (Professor Mosby, Dr. Eggvin, and Professor Ruud) and also the Masters and crews of the vessels are to be congratulated on the fact that the Norwegian ships are used so well.

K. M. R.

W. R. Ricker. "Stock and Recruitment". Journ. Fish. Res. Board Canada, **11**, 5, pp. 559—623, 34 figs. Ottawa, 1954.

In this valuable contribution to the literature of population studies the author discusses the role of natural mortality in the control of population size. He first distinguishes two types of natural mortality: (1) that which operates independently of the size of the population, termed density-independent or non-compensatory natural mortality; and (2) that which either increases (compensatory) or decreases (depensatory) with increase in population size, termed density-dependent natural mortality. The assumption is made that while the first can operate on all life history stages, the second only operates on the young immature members of the population, and on the basis of this assumption, a number of hypothetical models are built up. These models relate the sizes of the recruit populations to those of the parent populations, in both virgin and exploited stocks, under the influence of the two types of mortality operating alone and in combination.

The effects of some possible forms of compensatory mortality are described by a number of "reproduction curves", in terms of the number of eggs laid by the parent stock in any year and the number laid by the filial generation throughout life. The changes in the numbers in exploited and virgin populations in successive years are then determined for single- and multiple-age spawning populations under the influence of each type of reproduction curve, both in the absence of and in combination with density-independent mortality.

The results of this exercise show that some form of compensatory mortality is necessary to attain stability in population numbers. It is shown that stability is never reached in populations subject to density-independent mortality alone; they are subject to random fluctuations, often violent, which may lead either to extinction (in single-age spawning populations) or to limitless increase in numbers (in multiple-age spawning populations). Compensatory mortality sets an upper limit to total population size and results in the attainment of an equilibrium level or of a cyclic periodicity about a mean level, according to the precise form of the reproduction curve for the population. The effect of density-independent mortality superimposed on compensatory mortality (which is the condition applicable in almost all natural populations) is to introduce random deviations from the steady state for those populations which attain an equilibrium level under the influence of compensatory mortality, and to mask the periodicity of those which exhibit cyclic variations. The degree of masking and the extent of departure from a steady equilibrium will of course depend on the relative magnitudes of the two mortality components and of the age structure of the spawning stock and the age of first maturity. As the author points out, any number of population sequences can be derived by varying the form of the reproduction

curve, the magnitude of density-independent mortality, and the structure of the spawning population. The presence of exploitation does not affect the stability of the "equilibrium" populations, but it decreases the amplitude and period of oscillation of the populations subject to cyclic periodicity, and intensive exploitation tends to smooth out the oscillations altogether.

The author then presents examples of reproduction curves for a number of fish and other animal species. Unfortunately none of the data available for fish populations are sufficiently extensive or sufficiently detailed for complete reproduction curves to be drawn. However, the data for the Georges Bank haddock populations in the years 1912 to 1929 are cited as an example of a reproduction curve having a descending right-hand limb and therefore one which results in periodicity in abundance. This can be traced in the catch statistics from this fishery. In the author's opinion, dome-shaped reproduction curves are the ones which apply in most natural populations, although he considers that the flat-topped curve may apply in some situations.

In a final section the author develops a "theory of predation" in which a family of dome-shaped reproduction curves are derived from simple assumptions involving random cannibalism or compensatory predation. This family of curves includes most of the ones actually drawn from observed data, but the author shows that this typical form could be radically changed in practice.

This paper is the first in fisheries literature in which an attempt is made to analyse in detail the role of compensatory mortality in fish population dynamics. It illustrates clearly that compensatory mortality *must* operate at some stage in all natural populations, and it gives some clue as to the ways in which it may operate. As the author remarks, there is a great scarcity of — and a very great need for — really adequate observational data from which to determine the reproduction curves of existing fish populations and so to determine the types of oscillations to be expected in the population. Not until this is possible can the observed fluctuations in stock abundance be fully analysed.

B. B. Parrish.

J. S. Joensen. "On the life history of halibut in Faroe waters". Medd. Danmarks Fisk.- og Havunders., N. S., **1**, 5, 25 pp., 7 figs. København, 1954.

In this paper the author presents length measurements and age determinations of halibut caught in waters round the Faroe Islands. The bulk of the material refers to fish of age-group IV and over. These were taken on the coastal banks and in deep water in all seasons of the years 1938—39 and 1945—52 by the Faroese commercial longline fishery. A small quantity of data is also represented for the years 1908—52, from the fjords and bays as well as the banks. This material, which refers chiefly to the younger age-groups, was collected mostly in the summer by research vessels, the gear used being otter-trawl, lobster-trawl and eel hand-seine.

The author deals with each of the lower age-groups in turn. No specimens of the 0-group were found. The I-group occurred only rarely in the catches in spring and early summer, but was caught in fair numbers later in the summer in the bays and on coastal banks. Group-II fish were relatively abundant in fjords and bays and on the banks, while group-III fish were also found in all those localities. The author suggests that halibut at the age of three years begin to migrate from the fjords and bays; that they grow more rapidly on the banks than in the fjords; and that the decrease of group-

III as compared with group-II fish on the banks could be caused by intensive trawling. He readily admits, however, "that scant material prevents definite conclusions from being drawn." Indeed, it is particularly dangerous to make generalizations about the first few age-groups of Faroe halibut even on the basis of large samples. The reviewer has recently found considerable variation in the times at which group-II fish become available to the commercial fishery on the banks, and great fluctuations in growth and numbers of group-II and -III fish with season and year.

With regard to age-groups IV and over the author has a more adequate coverage, presenting 1803 measurements and 326 otoliths from a 10-year period. The material comes from two areas, one south of Syderø and the other extending on each side of Sandø. He shows that in general, age for age, females are longer than males, and since his data indicate that for both males and females, northern fish are bigger than southern fish of the same age, he concludes that there is a difference in growth-rate between the two areas.

Since the section of the paper on the older fish is best supported by data, it is unfortunate that it did not receive fuller treatment. All the observations from 1938—39, 1945—48, and 1950—52 are lumped together in one table (Table 10) and although it is possible to work out (with Table 1) that sampling was slight in 1945 and at maximum intensity in 1946, it is difficult for the reader to assess the validity of the size differences noted. A more detailed analysis of particular years would have been of interest.

As a result of his observations on halibut from the Faroese commercial longline fishery, the author puts forward the interesting theory that there may be two populations of halibut at Faroe, originating respectively from the areas north and south of the submarine ridge Faroe Bank — Bill Bailey's Bank — Lousy Bank. In view of the known extensive migrations of halibut one might be inclined to doubt that two populations living less than one hundred miles from each other on the Faroe plateau would remain sufficiently distinct to leave traces, discernible by length measurements, of a different origin. Nevertheless, the theory is a stimulating one, and will lead to a re-examination of existing data on halibut.

A. D. McI.

G. C. Bolster. "The biology and dispersal of *Mytilicola intestinalis* Steuer. A copepod parasite of mussels". Min. Agric. Fish., Fish. Invest., Ser. 2, **18**, 6, pp. 1—30, 5 figs., 2 pl. London, 1954.

Since the parasitic copepod *Mytilicola intestinalis* brought disaster to the Zeeland mussel farmers in the year 1950, shellfish biologists have paid due attention to its dispersal and biology in those countries of western Europe where mussels are of economical importance. It is of considerable value that the data collected are published without delay, for a comparison of conditions prevailing in various countries leads readily to the understanding of the entire complex biological pattern.

The present report demonstrates that the dispersal of *Mytilicola* in British waters is no longer limited to the east and south coasts of England, but that this parasite now occurs locally on the west coast of England and Wales, although almost exclusively in and near the shipping ports and shipbreaking yards. This finding fully confirms the view that *Mytilicola* does not easily extend its range without human interference. Though *Mytilicola* does have pelagic larvae, one should not conclude that it will therefore be able to extend its range in any direction. Though the free-swimming copepodid-stage

may, under laboratory conditions, live for as long as fifteen days, and may therefore be carried by currents over considerable distances, the chances of a new centre of infection being established are very limited, since such is only possible when a male and a female meet in the intestinal tract of one and the same mussel, the chances of which decrease with the distance the larvae are carried. Furthermore, as the number of eggs produced is limited to a few hundred at a time (which is very few for a parasite), and the life-span of each individual parasite is limited, one egg-bearing female is by no means certain to establish a new colony even in a rich population of uninfected hosts. Bolster therefore is certainly right when he concludes that the spread of *Mytilicola* other than by human agency is slow. Only where uninterrupted mussel beds occur can it spread very rapidly. Of much greater importance is the spreading by transport of infected hosts on shipping or by relaying of infected hosts in uninfected mussel areas.

The evidence put forward in this report demonstrates clearly that there is little hope that ecological conditions will prevent *Mytilicola* from infecting mussel populations on the British coasts which are so far uninfected. Earlier investigators believed that *Mytilicola* would only be dangerous under estuarine conditions, but both its occurrence in the highly saline Mediterranean waters and laboratory observations under reduced salinity indicates the hardiness of this creature. Comparison of infection rates in the Blyth estuary demonstrates a reduced intensity in both the upper reaches and near the mouth, which is explained by Bolster in terms of preferences for certain salinities. One should, however, bear in mind that the saline water bearing the larvae bathes the mussels in the upper reaches for a limited number of hours only, and that truly marine water, practically devoid of larvae, will be found near the mouth of the estuary for part of the time. This makes it clear that infection chances are highest in the central part of the estuary. Bolster's findings are therefore no proof that intensity of *Mytilicola* infection in the Blyth estuary is an indication of its salinity preferences.

Bolster's considerations on the vertical distribution pattern are also open to doubt. Exposure at low tide, and thereby a limitation in the number of hours that infection is possible, cannot be the main reason for heavier infestation of mussels in deeper waters, for the reviewer has observed the same phenomenon in mussel samples collected at increasing depth from one and the same plot, but all well below low-water mark. It would therefore seem that Hockley's suggestion that it is the positive geotropism of the copepodids which brings about the vertical distribution pattern, is more likely to hold good. Since currents are usually stronger rather than weaker in deeper waters, it does not seem probable that current velocity was the limiting factor here.

Bolster rightly ascribes anomalies in the observations on the breeding season to differences in water temperature during the winter. From observations on egg-bearing females Bolster concludes that 6°C. is the critical temperature for breeding in *Mytilicola*. Since the eggs are carried for some time, the appearance of new egg-sacs in spring might well be a better criterion by which to determine the critical water temperature. Using this criterion, the reviewer has found the critical temperature to be 7½°C., which, however, does not differ materially from Bolster's conclusions. In any case, interruption of the breeding season occurs only in waters where winter temperatures fall sufficiently low, and not on the English south coast and in northern Ireland. That breeding activities may vary considerably in the remainder of the season is not sufficiently stressed by Bolster. Observations in the

Netherlands demonstrate that intensity and success in breeding from spring to late in autumn are not closely linked with water temperature: evidently other factors have considerable influence.

It is interesting that oysters may be infected but that, even in places where *Mytilicola* is very numerous, oyster infection remains very light indeed. Damage to oysters is hardly to be feared, though oysters which are attacked decline in condition more readily than mussels.

The description of serious mussel mortalities after heavy *Mytilicola* infection at Whitstable, combined with repeated observation in the Netherlands of poor quality and mortality among mussels heavily infected by *Mytilicola* in the warmer season, makes it very hard to agree with D o l l f u s that *Mytilicola* is a harmless creature.

B o l s t e r gives little hope for control of this serious mussel pest, but it is the reviewer's experience that selection of rather shallow water for the cultivation of mussels (not necessarily above low-water mark) and careful planning of the quantities of mussels grown in a given body of water can lead to a fair biological equilibrium, rendering mussel cultivation possible even in the presence of *Mytilicola*.

P. Korringa.

Editorial Notice: the Current Bibliography

TO make provision for fresh developments and changes in emphasis in oceanography and fisheries science, a revised classification of the references in the Current Bibliography will be introduced in the first number of Volume 22. For the sake of continuity, efforts have been made to keep the alterations as few as possible. The principal changes are the reduction of the number of main headings from 12 to 9, the elaboration of heading 1), General Oceanography, and the combination of the headings Fish and Marine Fishery Investigations. For Physical Oceanography the system developed by the Association Internationale d'Océanographie Physique has been followed as closely as circumstances permit.

The details of the new classification are given below. The remarks which follow the secondary headings are explanatory only, not further sub-divisions.

Main Headings

1) General Oceanography and Fisheries
2) Physical Oceanography
3) Plankton
4) Benthos
5) Fishing
6) Fish
7) Shellfish
8) Mammals and Reptiles
9) Mischellaneous

1) General Oceanography and Fisheries

a) Expeditions

Voyage reports
Research ships

b) Navigation

Apparatus and systems
Navigational charts

c) Institutes

Annual reports

d) General Phenomena

Scattering layer
Underwater noise

e) General Apparatus

Underwater photography and television
Bathyspheres
Floating stations

f) General Textbooks

Textbooks
Tables

2) Physical Oceanography

a) Practical Aspects

General methods and apparatus (e. g., water-bottles)
Records of data

b) General Features of Oceans and Seas

Geographical extent
Names and limits of seas

c) Submarine Topography

Bottom deposits
Terminology
Bathymetric charts
Bottom sounding

d) Sea Water, Physics

Physical properties and their determination (e. g., temperature, density)
Suspended matter
Turbidity

e) Sea Water, Chemistry

Chemical and physical-chemical properties and their determination (e. g., salinity, nutrient salts, pH)
Pollution

f) Structure, Dynamics, and Circulation

Oceanography of particular sea regions
Distribution of properties of sea water
Turbulence
Stratification
Non-tidal currents
Interaction with atmosphere

g) Waves, Tides, and Sea-Level

h) Ice

i) Coastal Oceanography and Limnology

Fjords, estuaries, inland seas, and lakes

3) Plankton

a) General

Regional surveys (ecology and distribution)
Apparatus and methods

b) **Zooplankton**
c) **Phytoplankton**
d) **Nanoplankton**
e) **Productivity**

4) Benthos

a) **General**
- Regional surveys
- Apparatus and methods
- Production

b) **Fauna, Systematics and Development**
c) **Fauna, Distribution and Ecology**
d) **Fauna, Physiology and Behaviour**
e) **Flora**
- Diatoms
- Seaweeds
- Fungi

f) **Bacteria**

5) Fishing

a) **Statistical Returns**
b) **Vessels**
c) **Gear**
- Description
- Operation and efficiency
- Fish detection
- Experimental gear (e. g., electric fishing)

d) **Grounds and Fishing Surveys**
- Fishery charts

e) **Technology**
- Treatment of fish at sea
- Spoilage at sea

6) Fish

a) **Cod**
b) **Haddock**
c) **Hake**
d) **Plaice**
e) **Sole**
f) **Halibut**
g) **Other Marine Demersal Species**
h) **Herring**
i) **Pilchard**
j) **Tunny and Mackerel**
k) **Other Marine Pelagic Species**
l) **Salmon and Trout**
n) **Eels**
m) **Other Freshwater Species**

o) General

Several species treated together

Each of the above headings covers the following subjects:—

Systematics
Distribution and ecology
Physiology
Parasites and diseases
Stock fluctuations
Selection by fishing gear
Marking
Fisheries
Hatcheries, aquaria, and culture

7) Shellfish

a) Molluscs

b) Crustaceans

The subjects covered are the same as for Heading 6)

8) Mammals and Reptiles

9) Miscellaneous

a) Mathematical and Statistical Methods

b) General

Current Bibliography.

Prepared by the Editor with the Assistance of Mr. A. E. Margetts.

NOTE. The scope of the Bibliography is limited in the main to the area covered by the Council's activities, but there are included papers of general interest relating to other areas in North Temperate and Arctic regions and exceptionally elsewhere. Limnological references are not as a rule given, but papers relating to brackish waters and to salmon and freshwater fish studied by the Council are included.

Subscribers and those on the distribution list will receive regularly upon application to the General Secretary copies of the Bibliography printed on one side of the page only, for use in making up card indexes.

The Editor will be glad to be advised of emendations and additions to the Bibliography.

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